STUDIES ON THERMOREGULATION AND METABOLISM OF HIBERNATING CHIPMUNKS

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

By

Edward B. Pivorun

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

Acknowledgements

My deepest thanks are due Dr. William D. Schmid for the guidance, help and encouragement with which he provided me during this study. Dr. William D. Schmid, Dr. Robert Maxwell and Dr. Judson Sheridan read the manuscript and provided helpful and stimulating comments. Dr. Robert Maxwell provided many helpful suggestions regarding the construction of the calorimeter.

This work was supported by the National Science Foundation through a research stipend at the Lake Itasca Biology Station during the summers of 1969,1970, 1971 and 1972. The Department of Zoology provided me with equipment and components for the transmitters and calorimeter.

I especially wish to thank my wife, Phyllis, for the help and patience with which she provided me.

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The thermoregulatory patterns of captive hibernating chipmunks (Tamias striatus and Eutamias minimus) were studied using surgically implanted temperature sensitive transmitters. The duration of bouts of torpor and arousal and the body temperatures attained during these bouts were measured under different ambient temperatures and photoperiods. Both Tamias striatus and Eutamias minimus from northern Minnesota display distict thermoregulatory patterns during the hibernation period characterized by bouts of torpor alternating with periods of normothermia. Eutamias minimus can be considered Strumwasser's Type I hibernator because this species enters hibernation very quickly with one decline in body temperature to the minimum level. Tamias striatus can be considered the Type III hibernator because this species displays the "test drop" phenomenon. In both species the duration of a bout of torpor increases with successive bouts to a maximum or "plateau" stage. The duration of a single bout of torpor during the "plateau" stage is temperature dependent for both species; i.e., the duration increases with a decrease in ambient (and body) temperature. Eutamias minimus, the smaller of the two species and a species which does not accumulate excessive fat reserves prior to or during the hibernation period, displays significantly longer durations of torpor bouts at a particular ambient (and body) temperature than Tamias striatus. Tamias striatus also seems to display a response to photoperiod: decrease

in photoperiod results in an increase in the duration of bouts of torpor.

Both species display an active control of the decline in body temperature during the entrance into a bout of torpor and of the increase in body temperature during arousal.

The calorimetric studies on Tamias striatus illustrate the profound drop in metabolic heat output that results during the torpid condition. Reductions from 88-98% of normothermic levels can occur during torpor at ambient temperatures of 9°C and 11°C.

Use of a gradient type calorimeter provided a rapid and continuous measurement of the metabolic energy loss of the torpid and aroused animal. The calorimeter was constructed from an aluminum pressure cooker, which served as a shell enclosing the animal, and of a gradient layer lining the shell, which served as a means of monitoring heat flux. This gradient layer was constructed of 20 mil thick epoxy fiberboard. The heat flux across this layer was measured by approximately 2000 copper-constantan thermocouple pairs wired in series. The output of the calorimeter was read as a millivolt output and was monitored on a chart recorder.

Introduction

The majority of the studies dealing with the hibernation of the Eastern and Least chipmunk, in fact, the majority of studies dealing with hibernators in general, ignore the fact that hibernation is made up of different stages, and that environmental factors such as temperature and photoperiod may have a profound influence on the hibernating animals. Most studies are filled with qualitative statements such as "the hibernating animal" or "after the animal had been in hibernation for a few days" and generally do not consider the thermoregulatory patterns or stages of the hibernation period in a quantitative manner. The hibernating animal under study may be in quite different physiological or biochemical states during the initial stages of hibernation versus the latter stages. A delineation of the different stages of hibernation utilizing a simple to measure parameter such as core body temperature would be useful and essential in studies involving the physiology and biochemistry of hibernation.

In reference to the thermoregulatory patterns exhibited by hibernators, Strumwasser (1959a) characterized mammalian hibernators into at least three different types. Type I enters the hibernation period "very quickly". A long preparatory stage does not seem essential. Perognathus longimembris (Bartholomew and Cade, 1957) enters the hibernation period with one decline in body temperature to the minimum level within a few days following introduction to a cold environment. Type II enters the hibernation period after a long preparatory stage. Cricetus auratus (Lyman, 1948) enters the hibernation period with one decline in body

temperature to the minimum level after a one to three month sojurn in a cold environment. Type III enters the hibernation period after a relatively short preparatory stage. However, body temperature is not lowered to the minimum level in one decline. Strumwasser (1959a) was the first to report a detailed analysis of this pattern. He found that Citellus (Spermophilus) beecheyi began hibernation with a stage characterized by successive periods of torpor and arousal. Terminal body temperatures reached during each bout of torpor decreased until a minimum body temperature was reached which characterized the torpor periods following this initial stage. Strumwasser coined the term "test drop" stage for this initial phase of hibernation.

A few recent studies have provided information about the patterns of hibernation and the influence of ambient temperature on these patterns. Twente and Twente (1964, 1965a) have provided the most detailed information. They found that Citellus lateralis in the laboratory underwent a "test drop" stage. Moreover, the duration of successive bouts of torpor increased in a stepwise pattern. During the hibernation period, the bouts of torpor increased to a maximum duration (approximately halfway through the cycle) and then shortened until the final arousal of the hibernation period occurred. Most importantly, they found that the maximum duration of torpor showed a logarithmic relationship with ambient temperature.

Similar patterns have been shown to occur under laboratory conditions in Myotis lucifugus (Menaker, 1964), Erinaceus europaeus (Kristoffersson and Soivio, 1964), Citellus lateralis tesconum

(Pengelley and Fisher, 1961), Citellus citellus (Kayser, 1952), Perognathus longimembris (Bartholomew and Cade, 1957), Citellus tridecemlineatus and Citellus columbianus (Strumwasser et. al., 1964), Glis glis (Pengelley and Fisher, 1961), Eutamias speciosus (Jameson, 1964), and Eliomys quercinus (Pajunen, 1970). All these results were obtained either by using the imprecise sawdust method (Lyman, 1948) or implanted thermocouples. Wang (1973) utilizing radio telemetry observed similar patterns for Spermophilus richardsoni under natural conditions.

Very few qualitative or quantitative studies dealing with thermoregulation during hibernation have been undertaken utilizing the North American chipmunks. Both Woodward and Condrin (1945) and Forbes (1964) were not highly successful in inducing torpor in the Eastern chipmunk under laboratory conditions and no information regarding thermoregulatory patterns was obtained. Panuska (1959) was the first to observe that the hibernation of the Eastern chipmunk was made up of different stages. Panuska found that ordinarily a week or two of semitorpidity preceded the first deep torpor bouts of hibernation and that the animals periodically aroused from torpor. Neumann (1967) reported that the torpor of the Eastern chipmunk was generally sporadic and did not extend much beyond 24 hours in length. Moreover, he found that torpid animals at ambient temperatures between 0°C and 10°C never let body temperatures fall below 7°C. Wang and Hudson (1971) found that the Eastern chipmunk displayed torpor bouts one to three days in length at ambient temperatures of 4°C to 15°C, and torpor bouts less than two days in length at temperatures of 1.5°C to 3°C. Scott and Fisher (1972)

reported the first detailed information regarding the effect of ambient temperature on the duration of torpor in the Eastern chipmunk. They found that on the average the duration of torpor was 1.41 days longer at 0°C than at 18°C.

Much less work has been done on the hibernation of the chipmunk genus Eutamias. Cade (1963) published the first observations on the torpor of various species from this genus. Torpor was not noted in Eutamias quadrimaculatus. One individual of Eutamias amoenus became torpid and one individual of Eutamias speciosus was found torpid with a body temperature of 4.6°C. Cade concluded that the species studied probably do not use hibernation as the main adaptation for survival during the winter. Jameson (1964) studied the patterns of hibernation of Eutamias speciosus. Eutamias townsendi and Eutamias quadrimaculatus at ambient temperatures between 4°-6°C. All three species displayed torpor with arousals occurring every 1 or 2 days near the beginning and end of the hibernation period and averaged 5 or 6 days during the middle of the hibernation period. Heller and Poulson (1970) studied hibernation in Eutamias alpinus, E. speciosus, E. amoenus and E. minimus and found that low temperature and dehydration induced torpor only during the winter months.

Since so little quantitative work has been done on thermoregulation during hibernation, it was decided to quantitatively examine the patterns of torpor and arousal that compose the different stages of the hibernation period of the Eastern chipmunk and of the Least chipmunk under both laboratory and field conditions. These two species were chosen for study since 1) both are exposed

to the harsh winters of northern Minnesota; 2) little is known of their thermoregulatory patterns during hibernation; and 3) both are common to northern Minnesota and easily trappable.

The recently introduced methodology of radio telemetry was employed in order to minimize disturbance to the hibernating animals.

Materials and Methods

Eastern chipmunks, Tamias striatus, and Least chipmunks, Eutamias minimus, were collected by use of National live traps in Itasca State Park, Clearwater and Hubbard Counties, Minnesota during the summer months of 1970, 1971 and 1972. During the three years of this study approximately 200 Eastern chipmunks and 30 Least chipmunks of each sex were housed separately in stainless steel cages measuring 30 cm x 20 cm x 13 cm until transferred to experimental conditions. The colony of animals was maintained from August until May. Food and water, provided ad lib, consisted of approximately 95% sunflower seed and 5% Purina rabbit and rat chow. The animals were weighed once a week on a Ohaus triple beam balance accurate to $\pm$ .1 gm. While confined to the animal room, the chipmunks were exposed to uncontrolled room temperatures ranging from 29°C in August to 7°C in January. Photoperiod was also not controlled and was approximately 12L:12D during the late summer and early fall and 10L:14D during the late fall, winter and spring.

Laboratory Studies:

Hibernation was induced in the laboratory by placing the animals into an environmental chamber (Controlled Environments, Model C608, Pembina, North Dakota). Temperature and photoperiod were varied but humidity was not controlled. The experimental animals were housed within plastic cages measuring 29 cm x 18 cm x 13 cm, because metal cages interferred with the signals broadcast from the transmitters. Water was provided ad lib but food

was restricted to 210 gm of sunflower seed for the duration of the stay in the chamber. This is the amount of food that the chipmunks normally consumed in three weeks at ambient temperatures of 20°C. A small wad of cotton that the animals normally used to form a nest around themselves was added to each cage.

Core body temperatures were monitored by use of temperature sensitive transmitters which employed a modified form of the blocking oscillator circuit of Mackay (1968, pg. 138) (Fig. 1). The original circuit had a temperature sensing range of approximately 20°C to 45°C. This unmodified circuit could not be employed for monitoring the temperatures reached during torpor because transmission ceased at approximately 20°C. However, by replacing the 1 megohm thermister in the circuit with a 300 kohm thermister and the RT930H transistor with a GE D26-E6 transistor, a temperature sensing range of approximately 0°C to 40°C was attained. The various components were soldered together and held in place with epoxy glue. Mallory Duracell PX-13 mercury batteries (1.45 volts) were utilized as the power source and were attached to the transmitters via two copper strips and heatless solder (Eccobond Solder 56C, Emerson and Cuming Inc., Canton, Mass.). With the batteries in place, the units were coated with two thin layers of a paraffin Elvax mixture. The Elvax vinyl resin (E.I. Dupont De Nemours and Co., Chicage, Illinois) was mixed with paraffin in a ratio of ten parts paraffin to one part Elvax to give the paraffin the extra strength and plasticity needed when working at temperatures near 0°C. The completed transmitters weighed an average of 5 gms, approximately four to five percent of the body weight of an average

Eastern chipmunk and ten percent of the body weight of an average Least chipmunk.

The units were then placed in an oven at 40°C for four days before they were calibrated in a circulating water bath. It was assumed that no large temperature gradients would exist within the experimental animals' abdominal region because of the vascular system and that a circulating water bath would approximate the conditions within the abdominal region. The interval between pulses was plotted against temperature in °C. The output of the transmitters was characterized by an increase in the interval between pulses with a lowering of temperature. When the units were removed from the oven, the power output of the batteries was relatively constant and calibration was stable for a long period of time. The maximum shift in calibration using the Duracell batteries averaged about .4°C over a period of three months.

The transmitters were surgically implanted in the abdominal region of the animal. Hypothermia was used as the anaesthetic. During anaesthesia the animals were confined to small cages which were lowered into vats containing crushed ice and water. The animals were retained in the ice water until all movement, except for slight twitchings of the vibrissae, ceased. In general the body temperature reached at this point was 10-12°C. The animals were then removed from the ice bath, shaved, and a 2.5 cm incision was made in the body wall, musculature, and peritoneum in the abdominal region. The transmitters were inserted through these incisions and allowed to move freely in the intestinal region. In all cases the transmitters became encapsulated with tissues growing

from the intestinal mesenteries. The animals recovered full motility within 15-30 minutes after the incisions had been stitched up. Because of the peripheral vasoconstriction caused by immersion in the ice bath, blood loss was negligible. Only 5 animals succumbed out of approximately 200 operations.

The output of the transmitters was received on inexpensive AM radios tuned to 1600 KHertz. The output signals from the transmitters were recorded automatically every 30 minutes on a stereo tape deck by using a 30 minute repeat cycle timer (General Time, Torrington, Conn.). Up to four pairs of signals from implanted transmitters were recorded consecutively on the right and left channels of the tape deck. The tapes were then played into an interval timer (Itron Model 650-1, Itron Corp., San Diego, Calif.) that provided a digital readout for the intervals between pulses of the recorded data. These data were then converted to body temperature from the calibration curve.

Field Studies:

During the fall of 1972 two wood and hardware cloth cages measuring 1 m x .5 m x .5 m were constructed and placed in an oak savannah at the Cedar Creek Natural History Area, Anoka County, Minnesota. An artificial burrow system was constructed of hardware cloth and buried underground. The burrow itself was 1 meter long, 7 centimeters in diameter, and extended down into the ground at a 45° angle. The nest chamber (30 cm x 15 cm x 15 cm) was located 80 cm below the surface. Since the freezing temperatures encountered during the winter months could interfere with the operation of the AM receivers, an auxiliary antenna system had to

be developed. The antennas used were constructed from wood boards measuring 24 cm x 12 cm x 2.5 cm. Approximately 500 cm of standard hookup wire was wound along the longitudinal axis of each board forming eight loops per antenna. One antenna was attached to the bottom of each nest chamber. Coaxial cable was used to connect the antennas with the AM receivers. As in the laboratory studies, a repeat cycle timer and a stereo tape deck were utilized to record the signals from the implanted transmitters.

One Eastern chipmunk was introduced to each cage for a period of three months beginning November 25, 1972 and January 7, 1973. Food and water were provided ad lib. Human disturbance was kept at a minimum. During the winter months snow was allowed to accumulate over the systems.

Results

As is probably the general rule for all hibernators, the thermoregulatory pattern of hibernation in the Eastern chipmunk and the Least chipmunk was found to consist of bouts of torpor that alternated with periods of arousal and maintenance of normal body temperatures. Although similarities were found between the two species, some major differences in the thermoregulatory patterns have been discerned in this study.

Tamias striatus

Laboratory Studies:

The Eastern chipmunk displayed an annual weight cycle with maximum weights occurring from October to March. Two distinctly different weight patterns were observed. One group of animals exhibited low body weights averaging 100 gms in the summer and maximum weights of 135 to 145 gms during the winter. Another group exhibited low body weights averaging 90 gms in the summer and maximum weights of 105 to 110 gms in the winter (Fig. 2). Male and female chipmunks showed no significant differences in average body weights.

Animals initiated hibernation during the months of November through April, but not during the months of September or October (animals were not tested from May through August). Once hibernation was initiated, individual animals were allowed to maintain the torpid condition for two to four months during the months of November through June. In all cases hibernation was artificially interrupted before the animals could complete their

natural hibernation period. The chipmunks did not start hibernation immediately upon entry into the cold room. A period of 14 to 600 hours (mean of 175 $\pm$ 54 (t * x standard error of the mean at P = .05) hrs) was required before hibernation began (Fig. 3).

The Eastern chipmunk was found to enter hibernation in a series of steps (Fig. 4). Each successive bout of torpor tended to be of longer duration until a "plateau" stage was reached. The "plateau" stage was designated to be that portion of the hibernation period in which the durations of successive bouts of torpor did not change more than eight percent. The core body temperatures attained during successive bouts of torpor also decreased in a stepwise pattern until a minimum body temperature was reached. The bouts of torpor occurring before this minimum were designated "test drops" (Strumwasser, 1959a). The minimum body temperatures were always maintained at a higher level than the ambient temperatures. However, this difference was never more than 1.5°C while the animals were exposed to temperatures between 13°C to 3°C (Fig. 5). At 0°C this difference varied between 6°C and 14.5°C.

In most cases, the "test drop" stage terminated before the "plateau" stage was initiated. At an ambient temperature of 13°C, from zero to three torpor bouts occurred before the "plateau" stage was initiated. At all the other temperatures tested, from three to seven torpor bouts occurred before the "plateau" stage (Fig. 6). This stage between the "test drop" and "plateau" stages

* t is value from student's t distn: $t_{\alpha/2}$ (d.f.) = n - 1

was designated the pre-"plateau" stage.

Ambient temperature and photoperiod influenced the pattern of entrance into hibernation and the duration of the arousal and torpor periods. The number of "test drops" that an animal experienced tended to increase as the ambient temperature decreased (Figs. 7 & 8). The duration of torpor bouts during the "test drop" stage tended to increase with each successive bout of torpor. However, the average duration of torpor during this stage was not significantly different under all ambient temperatures tested (Fig. 9). The transition to the post "test drop" stage was found to be more abrupt at the lower ambient temperatures. At 13°C and at 10°C the average duration of the first post "test drop" bouts of torpor was not significantly different from the last bout of torpor in the "test drop" stage. However, at 8°C, 7°C and 3°C ambient temperature, the first post "test drop" bouts of torpor were significantly different (Fig. 10 and Table 1). For example, at 3°C the average increase was from 25 hrs to 84 hrs as constrasted to the average increase of 22 hrs to 43 hrs at 13°C.

Under a photoperiod of 12L:12D, the duration of bouts of torpor during the "plateau" stage of hibernation showed a linear increase with decrease in ambient (and body) temperature from 17°C to 4°C (Fig. 11). The linear regression for this relationship is expressed by the equation $y = -5.56x + 139.9$ where y is duration in hours and x is body temperature. Conversely, as the ambient (and body) temperature was increased the duration of bouts of torpor decreased (Fig. 12). The duration of bouts of torpor under a photoperiod of 8L:16D also increased with a decrease in

ambient (and body) temperature (Fig. 13). However, at two of the three temperatures tested under this shortened photoperiod, a significant increase in duration was observed when compared to the previous photoperiod. The linear relationship between duration of torpor and ambient temperature broke down at 0°C. In fact, the duration at 0°C, that averaged 23 hrs (range of 19 to 29 hrs), was significantly less than at any other temperature tested from 16°C to 3°C. The temperature dependency from 16°C to 3°C held true when either the same or different animals were exposed to the different ambient temperatures.

The duration of arousal periods during the "plateau" stage showed a decrease as the ambient (and body) temperatures decreased from 13°C to 8°C (Fig. 14). However, an increase in duration was noted as the temperature was further decreased to 3°C. At 0°C the animals displayed arousal periods averaging 34 hrs (14 to 58 hrs), a significant increase over the lengths displayed at ambient temperatures from 16°C to 3°C. The average durations of the arousal periods during the "plateau", pre-"plateau", and "test drop" stages were not significantly different from each other (Fig. 14). Interestingly enough, most of the animals studied displayed two to four consecutive arousal periods varying by no more than one to two hours in duration, although variations up to eight hours occurred (Fig. 15).

The initial phase of the arousal period followed a sigmoidal curve as body temperatures increased from torpid levels to normal body temperatures. This initial phase was divided into three parts: 1) the gradual initial segment, 2) the rapid intermediate segment

and 3) the gradual final segment. During the initial segment body temperatures increased from initial levels by .5°C to 4.5°C under all ambient temperatures tested. In most cases, this gradual initial segment lasted approximately 30 minutes. However, as the ambient temperature was lowered a larger number of arousal periods showed initial segments of longer duration. In fact, at 3°C all initial segments showed durations lasting at least one hour and extending to three hours (Table 2 and Fig. 16).

During the intermediate segment, which lasted approximately 60 to 90 minutes body temperatures increased from initial levels by 14°C to 27°C. At 13°C and 3°C the exponential rates of temperature increase for individual animals were not significantly different for arousal periods in the "test drop" or post "test drop" stage. However, at 8°C and 7°C the exponential rate during the post "test drop" stage was always significantly faster (Fig. 17). All animals in the post "test drop" stage, that were exposed to an ambient temperature of 13°C and then 8°C showed a significantly faster exponential rate of arousal at 8°C. Most animals exposed to 8°C and then to 3°C, on the other hand, showed no significant increase at 3°C (Table 3).

During the final segment, body temperatures increased from initial levels by .5°C to 6.5°C. The final segment was maintained from 30 to 90 minutes.

A torpor bout was always initiated once normothermic body temperatures had fallen to 34°C. The decline in body temperature during a bout of torpor followed an exponential relationship from normal body temperature to within a degree or two of the minimum

body temperature reached. When the logarithm of body temperature was plotted against time a linear relationship was observed for all ambient temperatures tested (Fig. 18). Regardless of the ambient temperatures, the rate of cooling of a living animal entering torpor was always significantly slower than the rate of cooling for the same animal dead and initially heated to 37°C (Fig. 19). At 16°C, 13°C and 10°C no significant difference in the rate of cooling between bouts of torpor in the "test drop" stage and post "test drop" stage was observed. However, at 8°C, 7°C and 3°C one to three bouts of torpor during the "test drop" stage showed rates of cooling significantly slower than bouts of torpor during the post "test drop" stage (Fig. 20). At a single ambient temperature, individual animals showed no significant differences in the rates of cooling of individual bouts of torpor during the post "test drop" stage (Fig. 21). Moreover, individual animals frequently showed no significant increase in cooling rates during the post "test drop" stage when exposed to different ambient temperatures (Table 4). This was observed when the ambient temperature was either raised or lowered.

When individual animals that were exposed to a single constant ambient temperature were subjected to a rapid (within 30 minutes) increase or decrease in temperature to a new constant level, an immediate arousal frequently occurred. In all cases the first subsequent torpor bout was characterized by the lowest body temperature the animal would attain at the new ambient temperature. In other words, no new "test drop" stage was initiated by any of the animals. However, from zero to three torpor bouts were observed

before a new "plateau" stage was reached. Arousal was not initiated if the temperature change occurred during the first third of the torpor bout that the animal was experiencing. However, if the temperature change occurred during the second half of the torpor bout, arousal was always initiated. Interestingly enough, the duration of an arousal initiated by a temperature change or by a disturbance was almost always less than the average duration of arousal experienced under the ambient temperatures preceding and following the evoked arousal (Talble 5). In fact, the duration of 75% of the evoked arousals was equal to or less than the shortest duration experienced by the animals.

A Chi-square test of homogeneity was utilized to show if arousal and torpor periods were initiated equally during the light and dark portions of a day (Table 6). Under a photoperiod of 12L:12D, the observed distribution of arousals was not significantly different from expected. However, the observed distribution of torpor bouts was significantly different from expected. A greater number of torpor bouts was initiated during the light portion than expected. Under a photoperiod of 8L:16D, the observed distribution of arousals was significantly different from expected. A greater number of arousals was initiated during the light portion. The observed distribution of torpor bouts was not significantly different from expected.

Field Studies:

Both Eastern chipmunks introduced into the outdoor cages on November 25, 1972 hibernated. Only one animal hibernated of the two introduced on January 7, 1973. All three hibernating animals

initiated the first bout of torpor 37 to 44 days after being placed outside. The two animals removed on January 1, 1973 were still undergoing bouts of torpor. The one animal removed on March 18, 1973 had ceased displaying torpor for at least a week.

The ground temperature at the level of the nest chamber slowly decreased from approximately 6°C in November to a low of -4°C in the middle of February (Fig. 22). Bouts of torpor were observed when ground temperatures ranged from 0°C to -4°C. Snow was found on the ground from December 1, 1972 to March 15, 1973. During this period of time not one of the three chipmunks ventured to the surface.

All three animals underwent a "test drop" stage with 2, 10 and 13 bouts of torpor making up this stage. The lowest average body temperatures attained in the post "test drop" stage were 9.8°C (9.1°C-10.8°C), 10.7°C (10.1°C-11.0°C) and 11.7°C (9.9°C-12.5°C) (Fig. 23). Two of the three animals showed an increase in torpid body temperatures after undergoing the series of torpor bouts with low body temperatures (Fig. 23).

The three chipmunks did not undergo a typical "plateau" stage. Torpor bouts of the longest duration occurred while the animals displayed the lowest body temperatures (Fig. 23). These torpor bouts averaged 26.7 hrs (16-36 hrs), 21.2 hrs (15-30 hrs) and 16.2 hrs (10-24 hrs) in length. Arousal periods for the three animals averaged 21.9 hrs in length.

Eutamias minimus

Laboratory Studies:

Unlike the Eastern chipmunk, the Least chipmunk did not

exhibit a yearly weight cycle. This chipmunk maintained an average body weight of 40 to 50 gms throughout the year (Fig. 24). Male and female chipmunks showed no significant differences in average body weights.

During the three months tested, animals initiated hibernation only during the month of November, but not during the months of February or March. Once hibernation was initiated, the torpid condition was maintained for three to four months from November through February. In all cases hibernation was artificially interrupted before the animals could complete their hibernation period. Hibernation was not started immediately upon entry into the cold room. A period of 101 to 333 hours (mean of 165 hours) was required before hibernation began.

Unlike the Eastern chipmunk, the Least chipmunk always entered hibernation without a "test drop" stage (Fig. 25). The first bouts of torpor at ambient temperatures of 10°C and 7°C were characterized by the lowest body temperatures that the animals would attain and maintain throughout subsequent torpor bouts. Minimum body temperatures were always maintained at a higher level than the ambient temperatures. This difference ranged from .8°C to 1°C while the animals were exposed to the ambient temperatures of 10°C and 7°C.

As was observed for the Eastern chipmunk, each successive bout of torpor tended to be of longer duration until a "plateau" stage was reached. The "plateau" stage was arbitrarily designated to be that portion of the hibernation period in which a change of ten percent or less occurred between the durations of successive

bouts of torpor. The "plateau" stage was preceded by one to four bouts of torpor at an ambient temperature of 10°C. At 10°C the Least chipmunk displayed initial bouts of torpor significantly longer than the Eastern chipmunk due to the lack of "test drops" (Fig. 26).

Under a photoperiod of 12L:12D, the duration of bouts of torpor during the "plateau" stage showed an increase with a decrease in ambient (and body) temperature (Fig. 27). Since the animals were exposed to only two ambient temperatures, it is not possible to say whether this relationship is linear. Interestingly, the duration of torpor bouts during the "plateau" stage of the Least chipmunk was significantly longer than that of the Eastern chipmunk at the same ambient temperatures.

The duration of arousal periods during the "plateau" stage was not significantly different at the two ambient (and body) temperatures tested (Fig. 28). As found with the Eastern chipmunk, most of the animals studied displayed two to four consecutive arousal periods varying by no more than one or two hours in duration, although variations up to nine hours occurred (Fig. 29).

The initial phase of the arousal period followed a sigmoidal curve as body temperatures increased from torpid levels to normal body temperatures. As with the Eastern chipmunk this curve was divided into three segments. During the initial segment body temperatures increased from initial levels by 1.5°C to 4°C under the two ambient temperatures tested. This initial segment lasted for approximately 30 minutes. During the intermediate segment, which lasted approximately 60 minutes, body temperatures increased

from initial levels by 20°C to 27°C. All animals that were exposed to an ambient temperature of 10°C and then 8°C did not show a significantly faster exponential rate of arousal at 8°C (Table 7). During the final segment, which lasted approximately 30 minutes, body temperatures increased from initial levels by 1°C to 5°C.

The decline in body temperature during bouts of torpor expressed as $\log_{10}$ showed a linear relationship when plotted against time under the two ambient temperatures tested. The rate of cooling of an animal entering torpor was always significantly slower than the rate of cooling for the same animal dead and initially heated to 37°C (Fig. 30). At a single ambient temperature, individual animals showed no significant differences in the rate of cooling of individual bouts of torpor (Fig. 31). Moreover, individual animals frequently showed no significant increases in cooling rate when exposed to a different ambient temperature (Table 8).

When individual animals that were exposed to an ambient temperature of 10°C were subjected to a rapid (within 30 minutes) change in temperature to 8°C, no immediate arousals were elicited. Neither "test drop" nor new pre-"plateau" stages were initiated by any of these animals. No arousals were initiated if the temperature change occurred during either the first or second half of the torpor bout that the animal was experiencing. The Least chipmunk seemed to be a "deeper" hibernator than the Eastern chipmunk; ie., less prone to arousals.

Utilizing the Chi-square test of homogeneity, the Least chipmunk under a 12L:12D photoperiod was found to initiate torpor

and arousal equally during the light portion and dark portion of the photoperiod (Table 9).

Discussion

An annual body weight cycle has been shown to occur in hibernators such as Citellus (Spermophilus) lateralis (Pengelley and Fisher, 1963) and Erinaceus europaeus (Kristoffersson and Suomalainen, 1964) under constant ambient temperatures and photoperiod. These cycles have been shown to persist even after enucleation (removal of eyes) (Pengelley and Asmundson, 1970). Panuska (1959) observed an annual weight cycle in the Eastern chipmunk exposed to both constant and fluctuating ambient temperatures and photoperiods. Panuska also found that a few individuals did not show an annual weight cycle, as was found to be the case in the present study, and did not enter torpor readily. Johnson (1930) also demonstrated that obese Citellus tridecemlineatus enter hibernation more readily than those without excess fat reserves. Many authors (Snyder et. al., 1961; Tevis, 1955; and Jameson and Mead, 1964) have observed that under natural conditions younger and thinner animals tend to disappear later underground and presumably enter hibernation much later than the adult and more obese individuals. The fact that certain individual Tamias striatus and all individual Eutamias minimus did not show appreciable weight gains suggests that food storage over the winter months is extremely important for the two species. The lack of fat reserves of some Eastern chipmunks may place these animals at a disadvantage regarding hibernation behavior and survival. Unfortunately, little data regarding survival or food storage behavior of obese and thin animals exists.

Pengelley and Fisher (1963) described a yearly or circannual

rhythm of torpor in Citellus lateralis. Scott and Fisher (1972) and Heller and Poulson (1968) also observed a yearly cycle of torpor in the Eastern and Least chipmunks. In the present study Eastern chipmunks exposed to low ambient temperatures from September to April did not initiate torpor during the months of September or October. However, most individuals tested during the months of November through April did initiate torpor. These results concur with those of Scott and Fisher (1972) in that they imply that this species can begin the hibernation period only during a certain part of the year after hypothesized biochemical or physiological preparations have been completed.

The existence of a "test drop" and a pre-"plateau" stage during the hibernation period of Tamias striatus and the existence of a pre-"plateau" stage during the hibernation period of Eutamias minimus suggests that the physiological and biochemical preparations for hibernation continue once the hibernation period itself has begun. Strumwasser (1959b) proposed that at each "test drop" the temperature regulating mechanism is being informed of the state of preparation for hypothermia and controls the depth of each "test drop" accordingly. Twente and Twente (1967b) considered Strumwasser's interpretation untenable since most hibernators studied do not enter a new "test drop" stage upon exposure to new ambient temperatures. They suggested that the different temperature levels attained during the "test drop" stage are the result of a steady state between heat production and heat loss as modified by the action of hormones upon both processes and not dependent upon the testing of how well preparations have gone.

Hayden and Lindberg (1970) and Mrosovsky (1964) speculated that "test drops" are a useful preparation for the arousal from torpor rather than for torpor itself. Hayden and Lindberg working with various species of Perognathus and Mrosovsky working with the rat found that these mammals adapted to repeated hypothermias by rewarming themselves more effectively than after a single cooling.

Probably the best hypothesis regarding "test drops" is that of Hammel (1967). He proposed that "test drops" were a cyclic resetting of the temperature control in the preoptic region and were an exaggeration of normal fluctuations in body temperature characteristic of the sleep-wake cycle. Luecke and South (1972) proposed that entry into hibernation is characterized by a programmed successive suppression or inhibition of activity in the preoptic/hypothalamic regions controlling thermoregulation. Heath et. al. (1972) suggested that input from the recticular formation may alter the response of the hypothalamus toward temperature or to the input from the peripheral temperature receptors. Using these concepts, one could consider each "test drop" to be the result of a gradual desensitization or inhibition of the preoptic/hypothalamic regions toward low temperatures. Williams and Heath (1971) and Heller and Hammel (1972) have demonstrated that in hibernators such as Citellus lateralis and Citellus tridecemlineatus the preoptic/anterior hypothalamic regions are sensitive to direct thermode heating and cooling during arousal and normothermia. However, Heller and Hammel found that the hypothalamic regulator of body temperature was completely inactivated during torpor since displacement of the hypothalamic

temperature in a torpid animal over the range of 1°C to 13°C elicited no thermoregulatory response in the rate of heat production. Reactivation of the preoptic/anterior hypothalamic regulator was found to occur during the arousal process. Cooling the animal below 1°C resulted in an increase in metabolic output and arousal. Heller and Hammel concluded that temperatures below 1°C reactivated the preoptic/anterior hypothalamic region, and they designated temperatures below 1°C as alarm level temperatures which result in arousal from torpor. Luecke and South (1972) observed an increase in metabolism of torpid marmots (Marmota flaviventris) when ambient temperatures were lowered from 5°C to 1.6°C or .5°C. Their results imply either an active hypothalamic regulator during torpor or that the alarm level temperatures begin between 5°C and 0°C. In contrast to the results of Heller and Hammel, Strumwasser (1959b) found that Citellus beecheyi maintained brain temperatures at extremely constant levels (±0.05°C) while skin temperatures varied from 7.8°C to 8.4°C. From the above one might therefore suggest that the actual cause of the decrease in metabolism, heart rate and other parameters of torpor may be controlled by the CNS and/or blood-borne humoral substances (Dawe and Spurrier, 1969, Dawe et.al., 1970), but that the level of inactivation or desensitization of the preoptic/hypothalamic regions may determine the level to which body temperatures can be lowered. Unfortunately experimental manipulations of the temperature of the preoptic/hypothalamic regions during the "test drop" stage have not been reported.

If "test drops" are the result of a programmed successive

suppression or inhibition of the preoptic/hypothalamic regions, one would expect that the lower the ambient temperature, the greater the number of "test drops" experienced. The Eastern chipmunk did, in fact, tend to show an increase in the number of "test drops" as ambient temperature was lowered. The large significant increases in the average durations of the first bouts of torpor during the post "test drop" stage over the last bouts of torpor during the "test drop" stage at the ambient temperatures of 8°C, 7°C and 3°C (Fig. 10) could be the result of a final resetting or desensitization of the hypothalamic thermostat.

Unfortunately, all papers dealing with the patterns of thermoregulation during hibernation ignore or fail to quantify the "test drop" stage and its relationship to ambient temperature. In fact, most papers fail to present the duration of successive bouts of torpor with the body temperatures attained during each bout thus making it impossible to distinguish between the "test drop" stage and the pre-"plateau" stage. Regarding "test drops" in the Eastern chipmunk, Panuska (1959) observed that this species at an ambient temperature of 3°C always displayed one to two weeks of semitorpidity with body temperatures ranging from 32.2°C to 7.8°C before the first bout of torpor. True torpor was characterized by heat rates of less than 20 beats per minute. Scott and Fisher (1971) observed only that successive bouts of torpor tended to increase in duration to a maximum while the animals were exposed to ambient temperatures of 0°C and 18°C. Regarding "test drops" in other species, Twente and Twente (1967b) demonstrated that Citellus lateralis at an ambient temperature of 5°C underwent two

to five "test drops". One individual did not undergo any "test drops" at 13°C, but at 5°C this same individual underwent three "test drops". Strumwasser et. al. (1964) stated that Citellus lateralis, Citellus tridecemlineatus, Citellus beecheyi, all underwent a "test drop" stage. Strumwasser et. al. (1967) observed 10 "test drops" for an individual Citellus lateralis at an ambient temperature of 5°C. Interestingly enough, Twente and Twente (1967b) observed large significant increases in the average durations of the first bouts of torpor during the post "test drop" stage. Utilizing their figures, one finds an average duration of 64 hrs for the last "test drop" and an average duration of 110 hrs for the first bout of torpor during the post "test drop" stage at an ambient temperature of 5°C. This again may signify a final resetting or desensitization of the hypothalamic thermostat. Twente and Twente also found that Citellus lateralis did not undergo a new "test drop" stage when exposed to new lower ambient temperatures. I found this also to be true for the Eastern and the Least chipmunk. These results may indicate that the hibernation period is characterized by a desensitization or resetting of the hypothalamic thermostat to temperatures lower then those reached during the post "test drop" stage. A desensitization down to alarm level temperatures may automatically occur during the early part of the hibernation period. Twente and Twente also found that handling animals during arousal caused many individuals to begin a new "test drop" stage. This might indicate a profound influence of the nervous or endocrine systems on the temperature sensitivity of the hypothalamic thermostat.

The Least chipmunk did not display any "test drops" at the one ambient temperature (10°C) tested. The lack of "test drops" suggests that this species can prepare itself physiologically or biochemically for torpor prior to the start of the hibernation period. Since the average time elapsed from placement into the cold room to the beginning of the hibernation period was 175 hrs for the Eastern chipmunk and 165 hrs for the Least chipmunk, preparation for the torpid condition did not prolong the start of torpor in the Least chipmunk. Thus, preparation for the torpid condition may have occurred prior to the experimental conditions and may normally be instituted sometime in late summer or fall. From an energetic viewpoint, the lack of "test drops" during the hibernation period is energetically advantageous and may have been selected for, along with the lack of fat reserves. Perognathus longimembris (Bartholomew and Cade, 1957) which weights 6.5 to 10 gms, also does not lay down excessive fat reserves for hibernation and also does not show a "test drop" stage. It may be a general rule that small mammals without excessive fat reserves do not exhibit a "test drop" stage. It would be interesting to look at the hibernating behavior of Zapus hudsonius and Napeozapus insignis, two small mammals which do lay down excessive fat reserves prior to the hibernation period (Morrison and Ryser, 1962), and the hibernating behavior of bats which in general do not lay down excessive fat reserves. Morrison and Ryser (1962) stated that Zapus hudsonius did show an instability of body temperature, with reductions to 29°C, when exposed to ambient temperatures of 0°C to 10°C. These may represent "test drops".

The fact that a pre-"plateau" stage exists and that the Eastern chipmunk in this study showed an increase in the number of torpor bouts during this stage as the ambient temperature was decreased suggests, as two possibilities, either that a further desensitization of the hypothalamic regulator occurs toward temperature or that a further desensitization occurs toward whatever the ultimate stimulus or stimuli are for arousal, be they biochemical or physiological. Regarding the pre-"plateau" stage of the Eastern chipmunk, Scott and Fisher (1972) observed a gradual lengthening in the duration of torpor as the hibernation period progressed. Twente and Twente (1967) observed that Citellus lateralis at an ambient temperature of 5°C underwent one to two bouts of torpor during the pre-"plateau" stage. One individual at 13°C did not undergo any pre-"plateau" bouts of torpor, but at 5°C this same individual underwent two pre-"plateau" bouts of torpor. One individual Citellus lateralis that Strumwasser et. al. (1967) studied underwent three bouts of torpor during a pre-"plateau" stage while at an ambient temperature of 5°C. Twente and Twente (1967b) found that Citellus lateralis did not undergo a new pre-"plateau" stage when exposed to new ambient temperatures, as was also the case for the Least chipmunk in this study. The Eastern chipmunk, however, was observed to undergo from zero to three bouts of torpor during new pre-"plateau" stages. Twente and Twente also found that handling animals during the arousal period caused many individuals to begin a new pre-"plateau" stage.

During the "plateau" stage both the Eastern chipmunk (from

16°C to 3°C) and the Least chipmunk (from 10°C to 8°C) displayed bouts of torpor which increased in duration as the ambient temperature was decreased. Unfortunately, a paucity of information exists in the literature on the influence of ambient temperature on the duration of bouts of torpor during the "plateau" stage. Wang and Hudson (1971) found that Eastern chipmunks spent from one to three days in torpor during the "plateau" at ambient temperatures from 4°C to 15°C and less than two days at temperatures of 1.5°C to 3°C. Scott and Fisher (1972) observed an average increase in duration of 1.41 days at 0°C as compared to 18°C. Neumann (1967) observed one individual with a duration of four days at an ambient temperature of 5°C. Panuska (1959) observed torpor at 3°C for up to one day, 110 times; for two days, 69 times; for three days, 42 times; for four days, 11 times; for five days, three times; and for six days, once. The fact that the studies of Panuska and Wang and Hudson failed to show an inverse linear relationship between ambient temperature and duration of a bout of torpor during the "plateau" stage, as was found in the present study, indicates that these authors did not differentiate the "test drop" and pre-"plateau" stages from the "plateau" stage and considered all torpor bouts equivalent.

Regarding the "plateau" stage of other species, Pengelley and Fisher (1961) and Fisher (1964) observed under a photoperiod of 12L:12D at 0°C to 2°C maximum durations of torpor for Citellus columbianus of 19 days, for C. tridecemlineatus 12 days, for C. lateralis 14 to 15 days and for Glis glis 33 days. Citellus lateralis was also observed to undergo torpor bouts five to six

days in length at 15°C and two to three days in length at 22°C. Strumwasser et. al. (1964) observed one individual Citellus lateralis with "plateau" torpor bouts 220 hrs to 250 hrs in length at an ambient temperature of 5°C. Kristoffersson and Soivio (1964, 1966) found that Erinaceus europaeus displayed maximum torpor bouts of 224 hrs to 322 hrs at an ambient temperature of 4°C and torpor bouts of shorter duration at 10°C. Eutamias specious (Jameson, 1964) exhibited maximum durations of six days at an ambient temperature of 5°C; Eliomys quercinus (Pajunen, 1970) 10 to 11 days at an ambient temperature of 4°C and a 24D photoperiod; and Myotis lucifugus (Menaker, 1964) 20 to 90 days at an ambient temperature of 4°C and a photoperiod of 24D. Twente and Twente (1967b, 1965b) utilizing Citellus lateralis found that, under least squares analysis, the relationship of duration of torpor during the "plateau" stage to ambient temperature between 2°C and 25°C was log hrs = 2.425 - 0.0405 body temperature. They observed variation among individuals, but generally animals which hibernated longer than the population average behaved similarily at all temperatures studied; average-period hibernators tended to exhibit durations near the population average; and short-period hibernators exhibited durations below the population average. The relationship between duration and ambient temperature was found to be the same under a photoperiod of 24D or 24L. However, photoperiod was shown to have an influence on the Eastern chipmunk in the present study and on Zapus hudsonius and Napaeozapus insignis in the study of Neumann and Cade (1964). In both studies, a shorter photoperiod resulted in longer bouts

of torpor.

The inverse relationship between duration of torpor during the "plateau" stage and ambient temperature broke down at 0°C for the Eastern chipmunk. This species showed a shorter duration at 0°C than at any other temperatures from 16°C to 3°C. This phenomenon was also observed with Erinaceus europaeus in that transferral of animals from a temperature of 4°C to -5°C resulted in torpor bouts of shorter duration (Soivio et. al. 1968). These results are probably due to an alarm temperature reaction. Too low an ambient temperature, and therefore too low a torpid body temperature, may reactivate the hypothalamic thermostat and cause an increased metabolism with maintenance of body temperature many degrees above ambient.

Both the Eastern chipmunk and the Least chipmunk maintained body temperatures approximately 1°C above ambient levels from 16°C to 3°C. At 0°C a difference of 6°C to 14°C was maintained by the Eastern chipmunk. Wang and Hudson (1970) reported differences from 3°C to 13°C for the Eastern chipmunk under ambient temperatures from 2.5°C to 25°C. These contradictory results are probably due to the fact that the "test drop" stage was ignored in the study of Wang and Hudson and all torpor bouts were considered equivalent. These small temperature differences are probably not due to an active thermoregulation but are equilibrium temperatures determined by the passive heat transfer characteristics of the body tissue and surrounding nesting material and the low metabolic rates maintained at the lower body temperatures as was shown by Hammel et. al. (1968) for Citellus lateralis. The large differences maintained at 0°C

probably represent an increased metabolism triggered when body temperatures fall below a certain critical level. Soivio et. al. (1968) found that Erinaceus europaeus maintained a higher metabolism and body temperatures at least 5°C above ambient temperatures of -5°C for up to three days. Pengelley (1964) reported that Citellus variegatus maintained body temperatures of 8°C to 10°C at ambient temperatures of -18°C.

The fact that animals periodically arouse from torpor and utilize approximately 90 percent of the energy expended over the hibernation period for the arousal process (Kayser, 1961) indicates that arousal is an important phenomenon during hibernation. Various theories have been advanced for the cause of these periodic arousals. Pengelley and Fisher (1961) observed that Citellus lateralis rarely ate extensively during arousal but always urinated. Further investigation showed that urine did not accumulate within the bladder as a torpor bout progressed, and it was therefore concluded that the filling of the bladder was not a stimulus for arousal. Since urine formation was found to be negligible in this species, it was concluded that the stimulus for arousal was a buildup of metabolic waste products within the blood system. This theory would account for the temperature dependency of duration, for torpor at lower temperatures would occur at lower metabolic rates and the production of metabolic waste products would be slowed down. The accumulation of metabolic products could probably directly or indirectly affect the nervous system and trigger an arousal. In fact, Heller and Hammel (1972) suggested that arousal is due to a sudden reactivation of the preoptic/anterior hypothalamic

regulator. As mentioned previously, the pre-"plateau" stage may represent a gradual desensitization of the nervous system to some metabolic products and the "plateau" stage may represent the maximum tolerance of the nervous system to the buildup of these products. Interestingly, the Q_{10} for the hypothesized process or processes controlling the duration of torpor for the Eastern chipmunk in this study and for Citellus lateralis (Twente and Twente, 1965b) was found to be between two and three, a value common to most enzymatic reactions.

The shortened bouts of torpor observed for the Eastern chipmunk at $0^{\circ}C$ could also be explained by this theory, for these animals were observed to maintain body temperatures at $6^{\circ}C$ to $14^{\circ}C$. Maintainance of body temperatures at this level would imply an increased metabolism of the animals and an increased buildup of metabolic products. Interestingly, Kallen and Kanther (1967) found that Myotis lucifugus produced urine while torpid. Mrovosky (1972) suggested that this ability may allow the species to clear its system of metabolic products and to remain torpid for up to 80 days (Menaker, 1964). Moreover, the average duration of arousal for the bats was approximately three hours, a value significantly lower than the 10 to 17 hrs reported by Strumwasser et. al. (1964) for Citellus lateralis; the 10 to 20 hrs reported by Twente and Twente (1967b) for Citellus lateralis; or the 13 to 21 hrs observed for the Eastern and Least chipmunks in this study.

In the few studies dealing with the causes of arousal, Pengelley and Fisher (1961), Fisher (1964) and Fisher and Manery (1967) proposed that arousal was due to an accumulation of urea

or blood electrolytes. However, Pengelley et. al. (1971) using aortic cannulation found no accumulations of urea, Na^{+}, K^{+}, or Ca^{++} in the blood during a bout of torpor. Moreover, Agid and Ambid (1969) and Galster and Morrison (1970) found a decrease in blood glucose in Glis glis and Citellus undulatus during the length of a torpor bout which was not observed in Citellus lateralis by Twente and Twente (1967b).

Various studies have shown that different substances can elicit arousal when injected intraperitoneally or into the blood system. Potassium chloride (Fisher and Mrosovsky, 1970) urea (Fisher, 1964) and adrenaline (Twente and Twente, 1968b) have all been shown to elicit arousal. However, one must be very careful in assigning the cause of arousal to a substance injected experimentally. Direct measurements of various substances during different phases of the torpor bouts have to be done in conjunction with experimental injections. Interestingly, Twente and Twente (1968a) found that intraperitoneal injection of .5 ml of isotonic saline produced no premature arousal during the first half of a torpor period, but always caused arousal during the second half of the torpor period. This same phenomenon was observed in this study in that individual Eastern chipmunks aroused prematurely because of a decrease in ambient temperature or noise only during the second half of the torpor bout. These results may suggest a gradual resensitization of the nervous system toward low temperatures, possibly due to the accumulation of metabolic end products or the depletion of essential metabolites. The fact that premature arousals of the Eastern chipmunk were generally of short

duration indicated that since the animals were not allowed to complete the full duration of torpor the full compliment of metabolic wastes was not produced, or that essential compounds were not utilized to as low a level as usual. This would allow for a faster filtration of the metabolic products from the blood, or a faster replenishment and therefore a shorter arousal period.

Strumwasser et. al. (1964) also proposed that arousal is the consequence of an increased sensitivity of the muscle and nervous systems to randomly released acetycholine packets. An increased sensitivity toward acetycholine normally occurs in denervated muscles, and one may be able to consider the muscles of hibernators as being functionally denervated during torpor. Lyman and Leduc (1953) proposed that arousal periods are necessary for food consumption. If food was denied to the hamsters thay were studying, death occurred. One could also think of arousal as being due to a depletion of some vital enzyme or to the gradual breakdown of important molecules or membranes. However, Willis and other workers (Willis et. al,, 1972) have shown that various hibernator tissues maintain normal membrane permeabilities and normal or enhanced $Na^+ - K^+$ - ATPase activities during torpor.

In the present study the Eastern chipmunk was found to have shorter bouts of torpor than the Least chipmunk at the same ambient temperatures. In other studies, the larger hibernators such as the ground squirrels were found to have shorter bouts of torpor than the smaller hibernators such as Glis glis and Myotis lucifugus. This suggests a general trend that the smaller the hibernator, the longer the individual bouts of torpor. This would seem reasonable

in that it would be energetically advantageous for a small animal without large fat reserves to spend the majority of the time in torpor. The shorter bouts of torpor exhibited by the Eastern chipmunk as opposed to typical hibernators such as the ground squirrels fits Neumann's (1967) conclusion that the Eastern chipmunk possesses a more primitive hibernation physiology.

Strumwasser (1960) and Heller and Hammel (1972) proposed that the decline in body temperature during entrance into a bout of torpor is not a passive cooling process. Strumwasser found that successive "test drops" of Citellus beechyi exhibited faster rates of cooling. Unfortunately the rate of cooling in the post "test drop" stage was not mentioned. Most interestingly, Citellus beechyi was found to exhibit "plateaus" and gentle steps of declining temperature as body temperatures decreased. Moreover, successive bouts of torpor exhibited cooling curves with shorter "plateaus" and larger amplitude steps of declining temperature. Heller and Hammel stated that their unpublished observations indicated that the decline in body temperature was due to a gradual drop in body temperature set point and hypothesized that the "plateaus" observed were due to this gradual drop. Strumwasser stated that the main braking mechanism seems to be intermittent muscle shivering.

In the present study the Eastern chipmunk showed significantly slower rates of cooling during the "test drop" stage as opposed to the post "test drop" stage at 8°C, 7°C and 3°C but equal rates of cooling at 16°C, 13°C and 10°C. In all cases the Eastern and Least chipmunk showed equal rates of cooling for bouts of torpor

during the pre-"plateau" and "plateau" stages. These results suggest not only a control over the rate of cooling but that the rate of cooling may depend on the amount of inhibition or desensitization of the hypothalamic thermostat. At the higher ambient temperatures, the hypothesized programmed successive desensitization of the hypothalamus or peripheral receptors may have progressed far enough that a brake on cooling rate greater than that observed for the post "test drop" stage is not operational. The fact that both Eastern and Least chipmunks often did not show an increase in the rate of cooling as the ambient temperature was lowered indicates that the rate of cooling may be controlled to a certain maximum rate for prevention of possible deleterious effects.

The Eastern chipmunk and Least chipmunk displayed sigmoidal rises in body temperature during arousal. This pattern has also been described for Mescricetus auratus (Lyman, 1965), Eptesicus fuscus, (Hayward et. al., 1965) and Perognathus hispidus (Wang and Hudson, 1970). Wang and Hudson (1971) also observed this pattern in the Eastern chipmunk. Their data (Fig. 32) regarding muscular activity during arousal suggests that shivering plays an important role during the rapid increase in temperature of the intermediate segment. They found that the intermediate segment was characterized by increased muscle electrical activity which indicates an increase in shivering. The initial and final segments were characterized by a decreased muscle electrical activity which indicates a decreased importance of the shivering process.

During the intermediate segment of arousal the Eastern chipmunk showed significantly slower rates of temperature increase at 8°C

and 7°C during the "test drop" stage as opposed to the post "test drop" stage, and equal rates of increase at 13°C and 3°C. This again implies a precise control of processes during hibernation. At 8°C and 7°C the processes controlling the rate of temperature increase may have to undergo a stage during which a greater efficiency of the heat producing mechanism is developed. At 3°C, the heat producing mechanisms may not have a chance to work more efficiently because of the low ambient temperature. This seemed to be the case even during the initial segment of arousal, in that at 3°C the initial segment of arousal was prolonged when compared to initial segments at higher ambient temperatures. The fact that the Eastern chipmunk increased the rate of temperature increase when ambient temperature was lowered from 13°C to 8°C, and the Least chipmunk increased the rate when the ambient temperature was lowered from 10°C to 8°C implies that the animals can control the production of body heat, so that normal body temperatures are reached within a certain period of time over a wide range of ambient temperatures. The fact that Eastern chipmunks did not increase the rate of heat production when temperatures were lowered to 3°C, implies that too low an ambient temperature may tax the heat producing systems of the animal.

Field Studies:

Wang (1973) observed hibernation of Spermophilus richardsoni under natural conditions using radio telemetry. This species was observed to undergo a "test drop" and "plateau" stage, but no pre-"plateau" stage. The "test drop" stage for the three individuals studied was prolonged for up to two months. Unlike

Citellus lateralis which under lab conditions exhibited durations of torpor of .5 days to 2 days during the initial "test drops", Spermophilus richardsoni exhibited torpor bouts four to six days in length. Unfortunately burrow and subterranean temperatures were not provided. Air temperatures were observed to vary between 15°C to -3°C in September and October and -3°C to -23°C from November through February.

In the present study, the Eastern chipmunk was also observed to undergo a "test drop" stage. However, a typical pre-"plateau" or "plateau" stage was not observed for these animals. The fact that the ground temperature ranged from 0°C to -4°C and the fact that the animals were restricted to a certain depth beneath the surface may have caused the animals to exhibit atypical torpor patterns. In fact all animals exhibited average body temperatures of 9.8°C to 11.7°C, which fell within the 6°C to 14.5°C range observed for laboratory animals at an ambient temperature of 0°C. The length of torpor bouts averaged 16.2 to 26.7 hrs, values which approximate the 29 hrs observed in the laboratory. These results indicate that the animals were probably exposed to temperatures below alarm levels.

GRADIENT CALORIMETRY

Introduction

The metabolic rate of the Eastern chipmunk, as measured by oxygen consumption, during torpor and arousal has been observed by Neumann (1967) and Wang and Hudson (1970). Neumann found that summer animals displayed a zone of thermal neutrality between 28°C and 36°C; while Wang and Hudson found this zone to exist between 28.5°C and 32°C. In both studies oxygen consumption at ambient temperatures below thermal neutrality was found to increase linearly according to the equation cc O_2 consumed/gm/hr = 4.4 - .11t, where t is the ambient temperature. Neumann observed that chipmunks torpid at temperatures from 7°C to 10°C possessed an oxygen consumption that ranged from .5 to .8 cc/gm/hr, approximately 15 percent of normothermic values. Oxygen consumption of animals torpid at temperatures from 15°C to 22°C ranged from .04 to .4 cc/gm/hr, approximately 2 to 15 percent of normothermic values. Wang and Hudson observed that chipmunks torpid at temperatures from 4°C to 24°C possessed an oxygen consumption that ranged from .06 to .74 cc/gm/hr, approximately 1.6 to 33 percent of normothermic values.

An important drawback with the use of oxygen consumption as a measure of metabolic rate is that it is an indirect measure of heat loss from the body. Before heat loss can be calculated from oxygen consumption values, the proportion of fats, carbohydrates, and proteins being metabolized by the animal must be known. Calculation of R.Q. values provides an estimate of the proportion of these three metabolites being utilized. Tables are available

which provide an estimate of the number of calories produced for each cc of O_2 consumed at a certain R.Q. Since many errors are possible utilizing this indirect calorimetric methology, it was decided to attempt a direct calorimetric measure of heat flux from Eastern chipmunks exposed to different ambient temperatures. A gradient calorimeter, similar in design to those of Benzinger and Kitzinger (1949), Lawton et. al., (1954) and Caldwell et. al., (1966) was constructed for use in this study.

Materials and Methods

The main sensing elements of the gradient calorimeter were the flux plates, and the theory behind the operation of the calorimeter was based on the Fourier heat conduction equation. The flux plates were constructed from 10 mil thick and one half inch wide serrated epoxy glass strips of constant conductivity (Cadillac Plastics, Minneapolis, Minnesota). Constantan wire (2 mil) was wrapped around the strips and positioned within the grooves of the serrated edges. One half of the width of each strip (both front and back) was then masked with nail polish. The masked strip was placed within a copper plating bath and the exposed constantan wire was plated following the methods of Tanner (1963). The point of contact between the unplated and the copper plated wire forms a copper-constantan junction. Therefore, each strip of epoxy glass had a series of copper-constantan junctions along the length of the constantan wire. The plated strip then consists of pairs of copper-constantan thermocouples connected in series with one member of each pair located on opposite sides of the epoxy glass strip and the temperature difference across the strip can be determined.

The Fourier heat conduction equation states that heat flux through a material is equal to the conductivity of the material times the temperature gradient across the material, divided by the distance of heat transfer through the material, or $q = k\Delta t/\Delta x$. To apply this equation to the flux plates, the following relationships can be stated: 1) the conductivity of the material is uniform and 2) the thickness of the material is constant.

Therefore, regarding the flux plates, the heat transfer equation can be rewritten as $q = C\Delta t$; i.e. heat transfer through the flux plate is directly proportional to the temperature difference across the flux plate (Fig. 33). The temperature difference is produced in the calorimeter by maintaining one side of the flux plates at a constant temperature and supplying heat to the other. This temperature difference can be measured by the copper-constantan thermocouples.

The shell of the gradient calorimeter was constructed from an aluminum pressure cooker. The inner surface of the pressure cooker was lined with flux plates connected in series and mounted on a 10 mil thick epoxy glass sheet which electrically insulated the flux plates from the metal sides. Once mounted into place the flux plates were coated with a thin layer of marine spar varnish to protect them from damage. A layer of flat black paint was added to assure maximum absorbance of thermal energy.

The completed unit was placed in a refrigerated, constant-temperature water bath. Air was drawn from a compressed dry air tank through a flask containing a measured amount of water. The rate of air flow into the calorimeter was maintained at 40 cc/min. Before the flow of air entered the calorimeter, it passed through copper coils submerged within the water bath to cool it to the temperature of the water. All air exiting the calorimeter passed through drying tubes containing Drierite to collect added moisture. The calorimeter was connected to a strip chart recorder.

The calorimeter was calibrated with an electric heater, which consisted of a 75 cm long piece of 2 mil constantan wire wound

around a 100 ml glass beaker. The output of the heater in watts (watts = I^2R) was converted to cal/min (watt = 14.33 cal/min). A calibration curve of calorimeter output (mv) as a function of energy input was determined. A series of curves was generated for differences observed with placement of the heater at different positions in the calorimeter.

The response time of the calorimeter was measured by placing a lighted 15 watt incandescent light bulb within the calorimeter and noting the time interval elapsed from the introduction of the bulb to a maximal mv output of the calorimeter.

Animals were placed within the calorimeter, without food or water, housed within a wire cage, and were exposed to ambient temperatures of 4°C, 9°C, 11°C and 14°C. The thermal output of the animal via radiative, conductive, convective and evaporative heat loss was recorded on the strip chart recorder and the heat loss per unit time was determined by integration of the recorded output with a planimeter.

Results

During calibration the response of the calorimeter in millivolts was found to be linear with thermal outputs from zero to 43 cal/min. The thermal output of Eastern chipmunks exposed to ambient temperatures down to 4°C fit within this range. The linear regression line constructed from points obtained during calibration was $y = 30.5x + .05$, where y equals the thermal output in cal/min and x equals the millivolt output of the calorimeter (Fig. 34). A plus or minus five percent variation around this line was observed with placement of the heater within different parts of the calorimeter. The amount of thermal energy carried out of the calorimeter by the air stream was found to be negligible. The rapidity of response of the calorimeter to thermal outputs was approximately 70 sec.

The heat loss of chipmunks exposed to temperatures between 14°C and 4°C was recorded as a constant minmal output interrupted by increased outputs lasting an average of 15 minutes. These periods of increased output seemed to occur in a random manner over a 24 hr period of time. During these short periods of time the thermal output from the animals increased up to 65 percent over the minimal values. Fig. 35 represents the relationship between ambient temperature and the minimal heat loss of the animals expressed in cal/gm of animal min. The linear regression for this relationship is expressed by the equation $y = .35 - .014t$, where y is the heat loss in cal/gm min and t is the ambient temperature.

Of the fifteen animals tested within the calorimeter, three animals entered torpor at the ambient temperature of 9°C and one

animal at the ambient temperature of 11°C. The minimal thermal output of the one torpid individual at 11°C ranged from .01 to .02 cal/gm min, approximately six to twelve percent of normothermic values. The minimal thermal output of three individuals torpid at 9°C ranged from .004 to .01 cal/gm min, approximately two to four percent of normothermic values.

Discussion

The calorimeter designed and constructed for this study proved to be a very satisfactory tool for the direct measurement of thermal loss from a living mammal. The use of a more uniform outer shell, without rivets and handles, would probably have reduced the plus or minus five percent variation in output to a lower level. The seventy second response time did not allow for measurement of fast changes in thermal output. However, this response time proved to be satisfactory for the measurement of the thermal output of the Eastern chipmunk, which displays constant levels for the majority of the time.

The fact that the animals in this study showed such constant levels of heat loss, which were occasionally interrupted by increased levels of heat loss, indicates a control of heat production. The periods of increased heat loss were probably periods of increased activity or the result of vasodilation. The linear increase of thermal loss with decreases in ambient temperature paralleled the results obtained from indirect calorimetry using oxygen consumption as a measure of metabolism.

Torpor was shown to result in a very substantial reduction of metabolic heat production. At ambient temperatures of 9°C and 11°C, torpor resulted in an 88-98 percent reduction in heat production as compared to normothermic values. The reduction in metabolic heat production obtained in this study compares favorably with those values obtained by Neumann (1967) and Scott and Fisher (1971).

Conclusion

Both the Eastern and Least chipmunk from northern Minnesota display distinct thermoregulatory patterns during the hibernation period characterized by bouts of torpor alternating with periods of normothermia. The Least chipmunk can be considered Strumwasser's Type I hibernator because this species enters hibernation very quickly with one decline in body temperature to the minimum level. The Eastern chipmunk can be considered the Type III hibernator because this species displays the "test drop" phenomenon. In both species the duration of a bout of torpor increases with successive bouts to a maximum or "plateau" stage. The duration of a single bout of torpor during the "plateau" stage is temperature dependent for both species; i.e., the duration increases with a decrease in ambient temperature. Interestingly, the Least chipmunk, the smaller of the two, and a species which does not accumulate excessive fat reserves prior to or during the hibernation period, displays significantly longer durations of torpor than the Eastern chipmunk. The Eastern chipmunk also seems to display a response to photoperiod: decrease in photoperiod resulted in an increase in the duration of bouts of torpor.

Both species display an active control of the decline in body temperature during the entrance into a bout of torpor and of the increase in body temperature during arousal.

The calorimetric studies of the Eastern chipmunk illustrate the profound drop in metabolic heat output that results during the torpid condition. Reductions from 88-98% of normothermic values can occur during torpor at ambient temperatures of 9°C

and 11°C.

The differences in the thermoregulatory patterns of the two species during the hibernation period indicates that the two species possess some important biochemical and/or physiological differences. An elucidation of the thermoregulatory pattern of different hibernating species would provide a basic framework for further biochemical or physiological studies that could unravel the basic secrets of the phenomenon of hibernation.

Fig. 1. Blocking oscillator circuit, after Mackay (1968)
T = GE D26-E6 transistor, B = 1.45 V Hg battery,
R_1 = 500 K ohm thermister, C_1 = .68 uF capacitor,
C_2 = 100 pF capacitor, L_1 = L_2 = 50 turns,
L_3 = 100 turns.

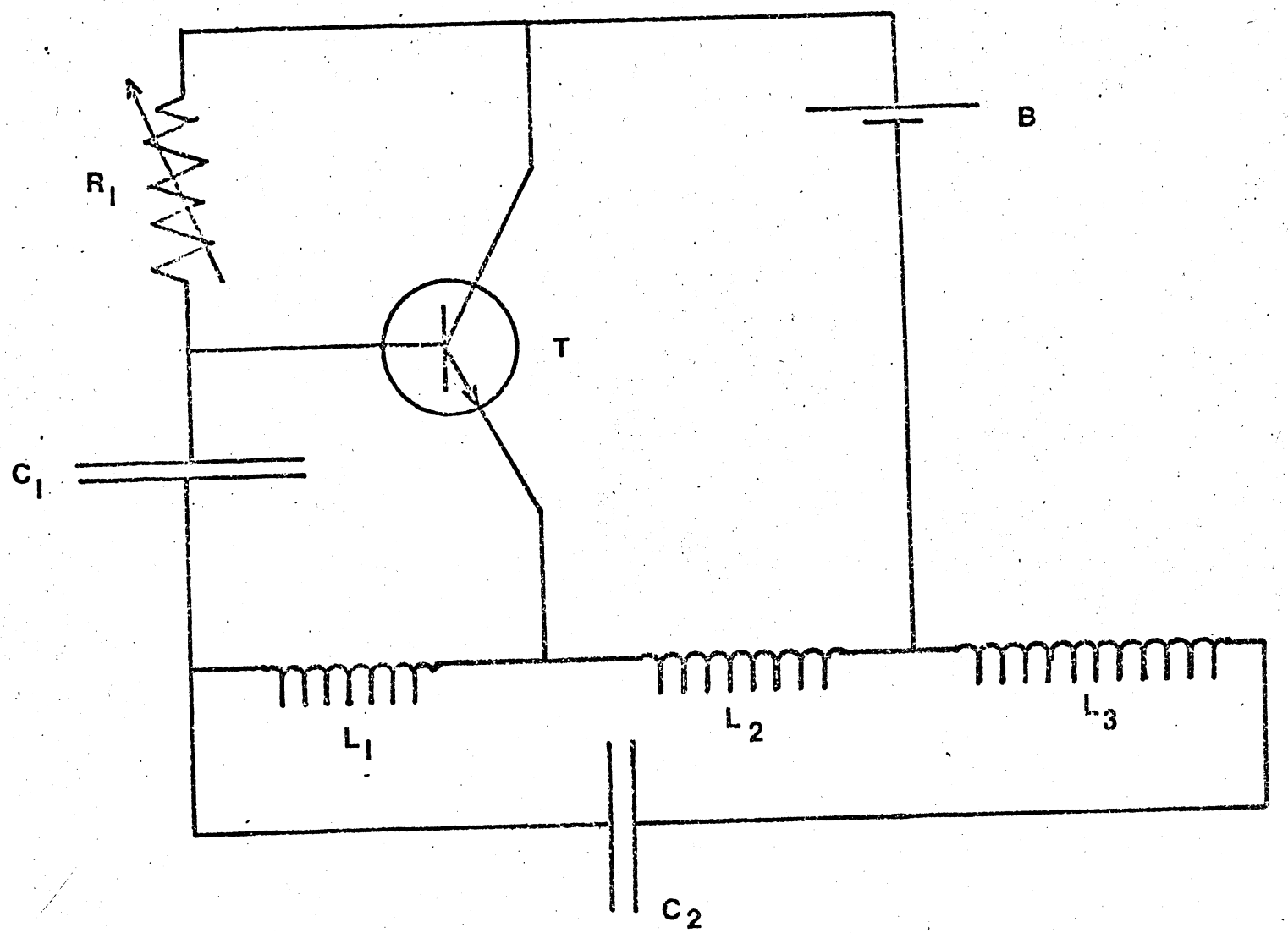

B
R_1
T
C_1
L_1
L_2
L_3
C_2

Fig. 2. Seasonal variations in the average body weights of Tamias striatus (1971-1972). Symbols represent mean body weights. Means of heavy weight group were found to be significantly different from means of light weight group at all points.

* Heavy weight group

⚙ Light weight group

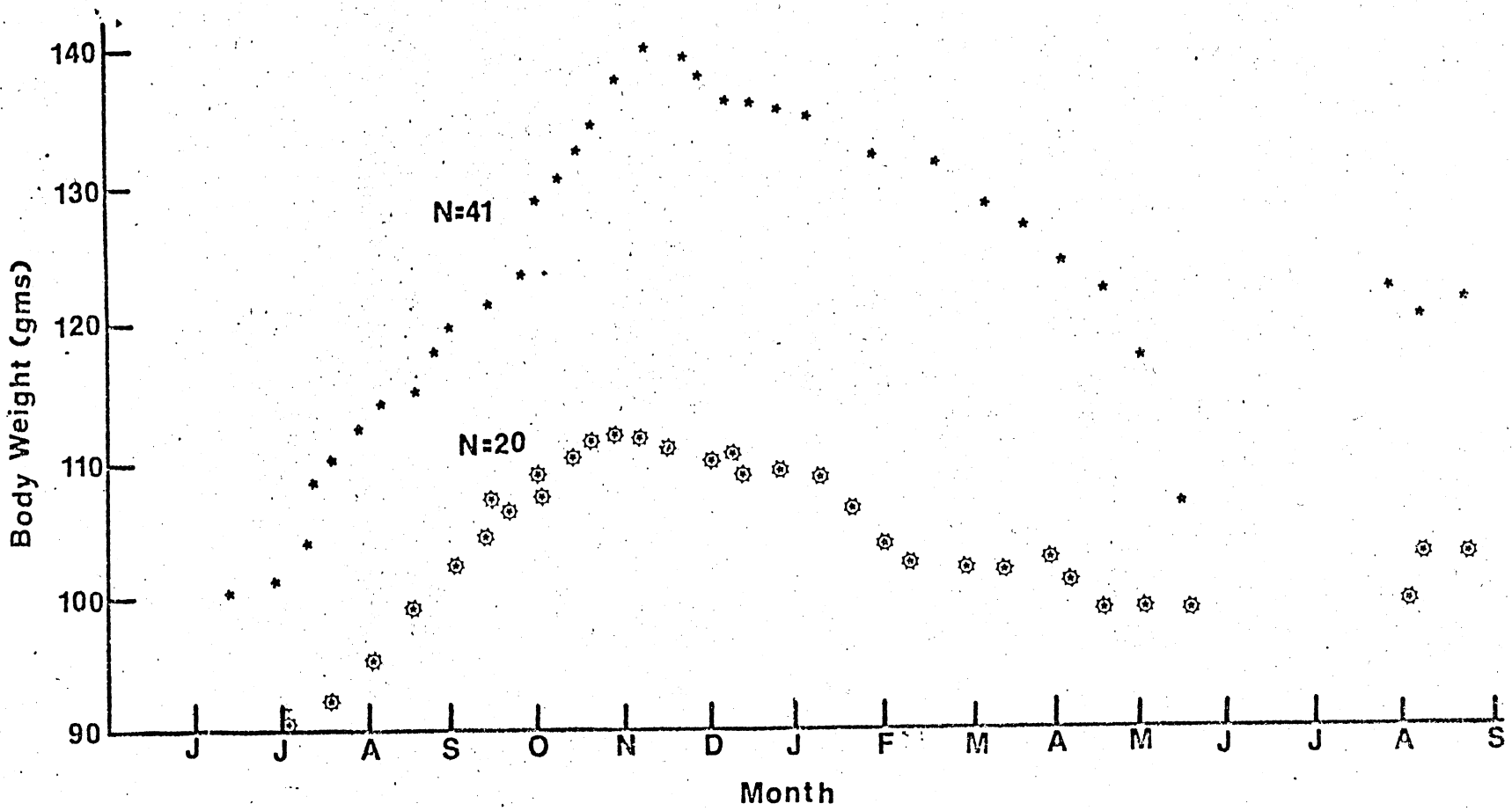
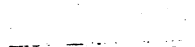

140
130
120
110
100
90
Body Weight (gms)
N=41
N=20
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

Fig. 3. Incidence of torpor.

Numbers indicate number of hours from entry into cold room to first bout of torpor.



Months tested during which torpor was observed for a single individual

Months tested during which torpor was not observed for a single individual

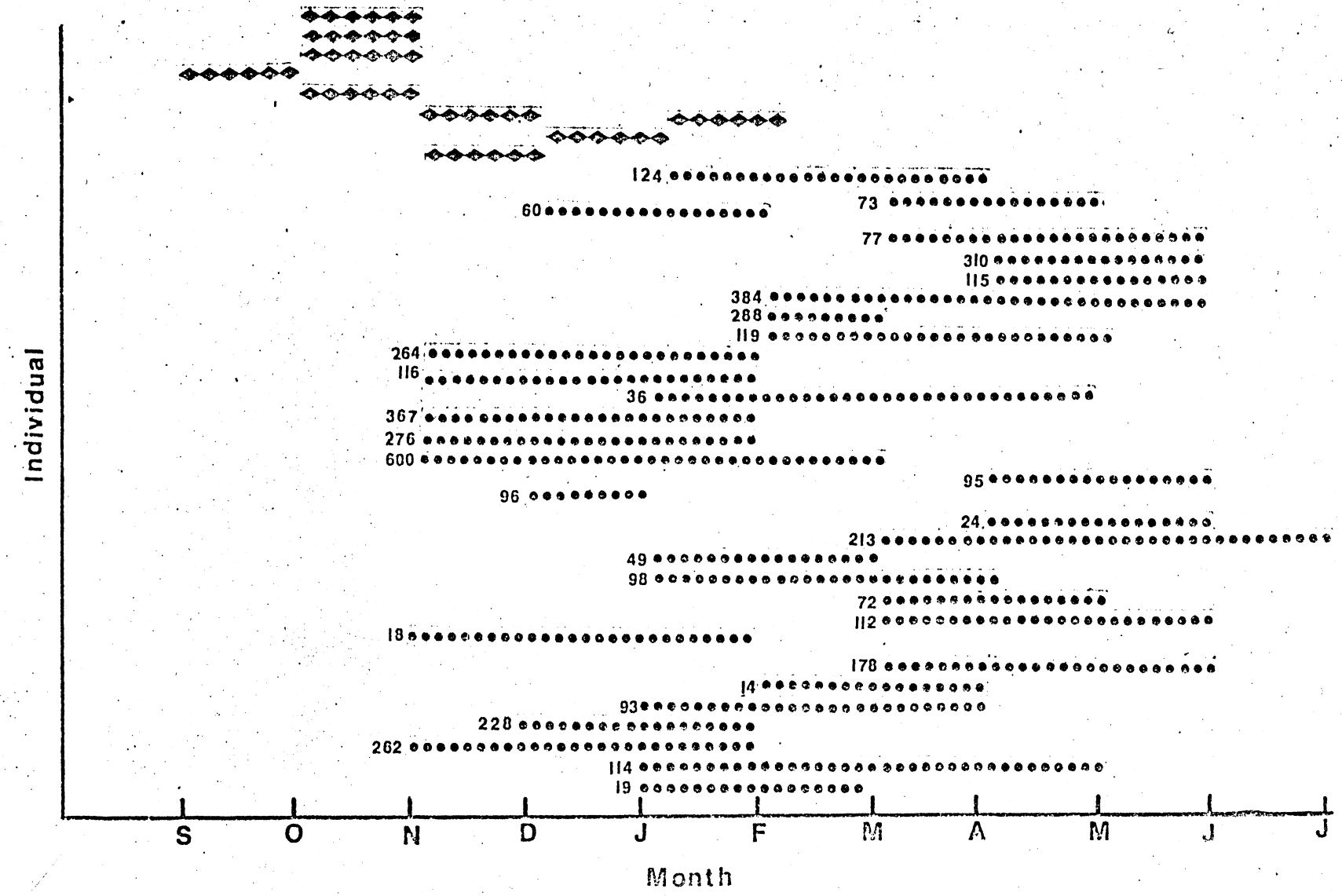

Individual
124
73
60
77
310
115
384
288
119
264
116
36
367
276
600
95
96
24
213
49
98
72
112
18
178
14
93
228
262
114
19
S
O
N
D
J
F
M
A
M
J
J
Month

Fig. 4. Thermoregulatory pattern of Tamias striatus during the hibernation period.

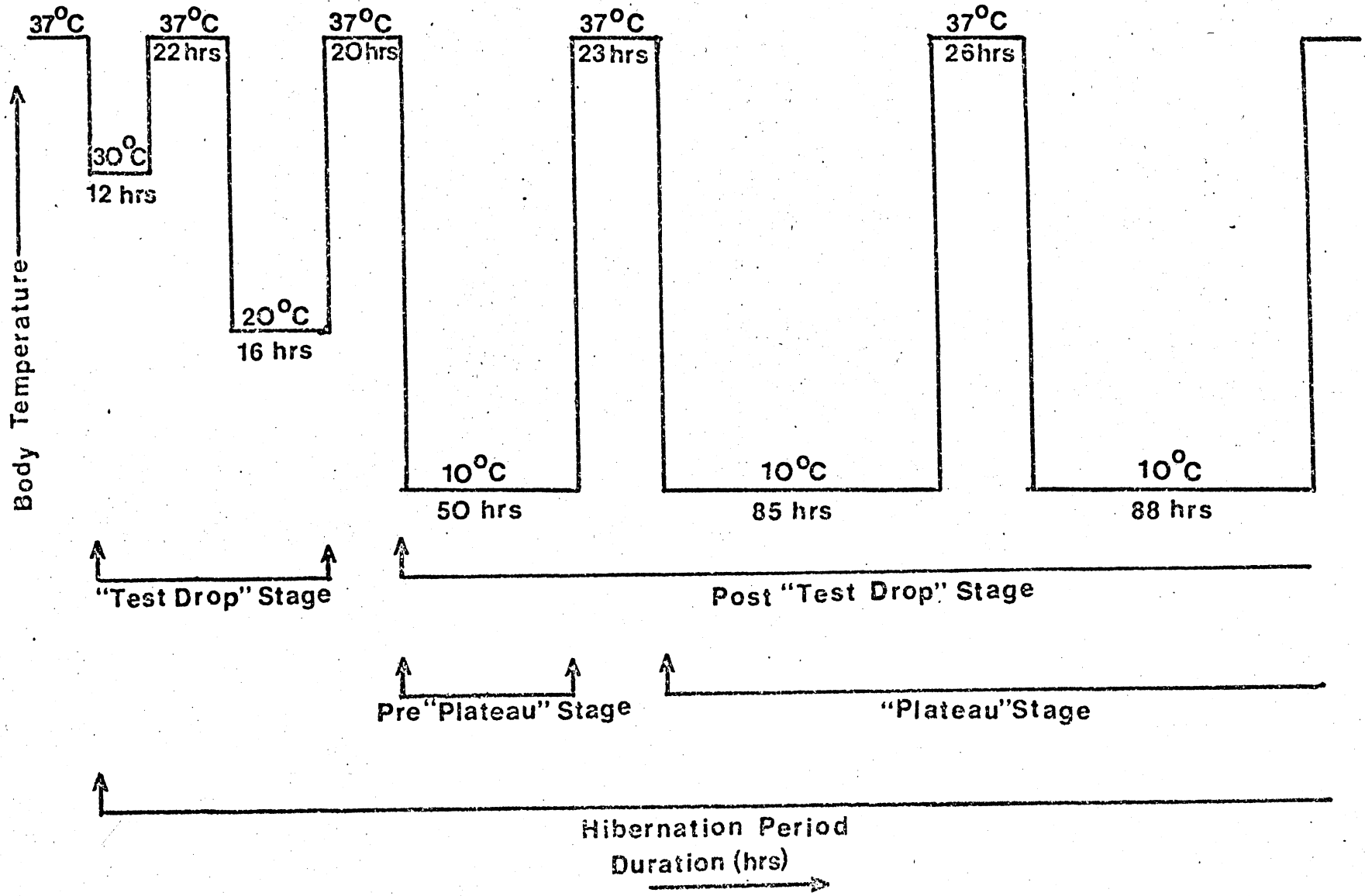
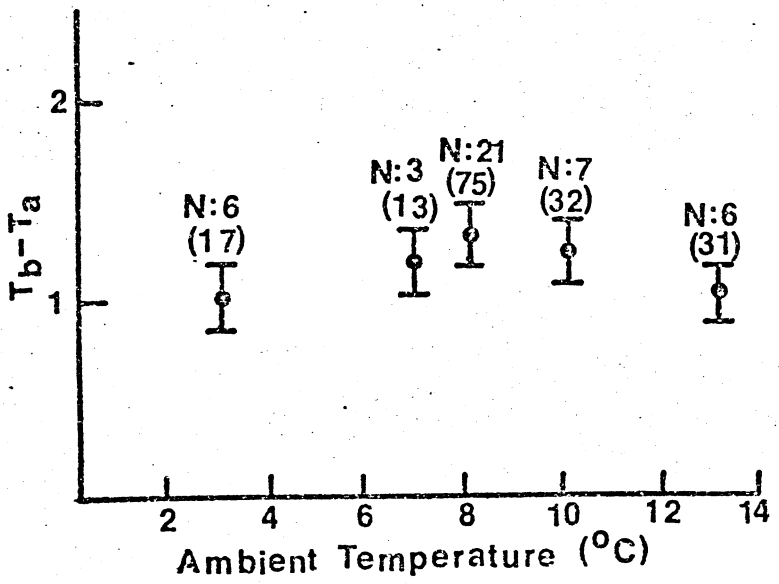

37°C
37°C
22 hrs
37°C
20 hrs
37°C
23 hrs
37°C
26 hrs
30°C
12 hrs
20°C
16 hrs
10°C
50 hrs
10°C
85 hrs
10°C
88 hrs
Body Temperature
"Test Drop" Stage
Post "Test Drop" Stage
Pre "Plateau" Stage
"Plateau" Stage
Hibernation Period
Duration (hrs)

Fig. 5. Difference between minimum body temperature and ambient temperature as a function of ambient temperature. N is the number of individuals and the number in parentheses is the number of observations.

Mean $\pm$ t x standard error of the mean at P = .05

Fig. 6. Relationship between the ambient temperature and the number of bouts of torpor during the pre-"plateau" stage.


$T_b - T_a$
2
1
N:6
(17)
N:3
(13)
N:21
(75)
N:7
(32)
N:6
(31)
2
4
6
8
10
12
14
Ambient Temperature (°C)

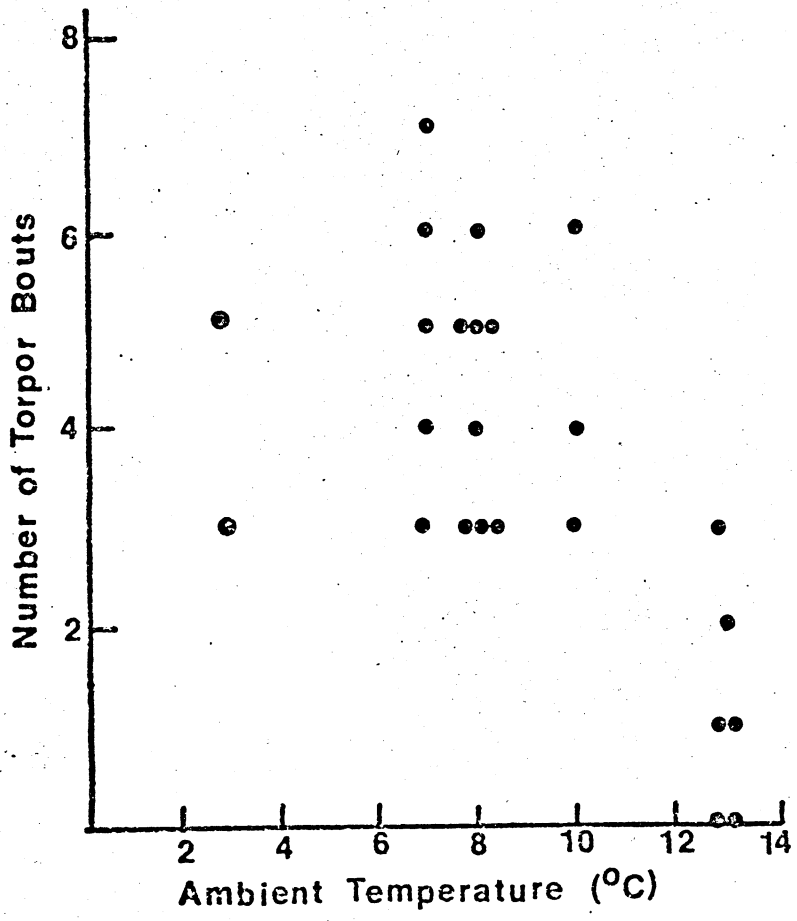
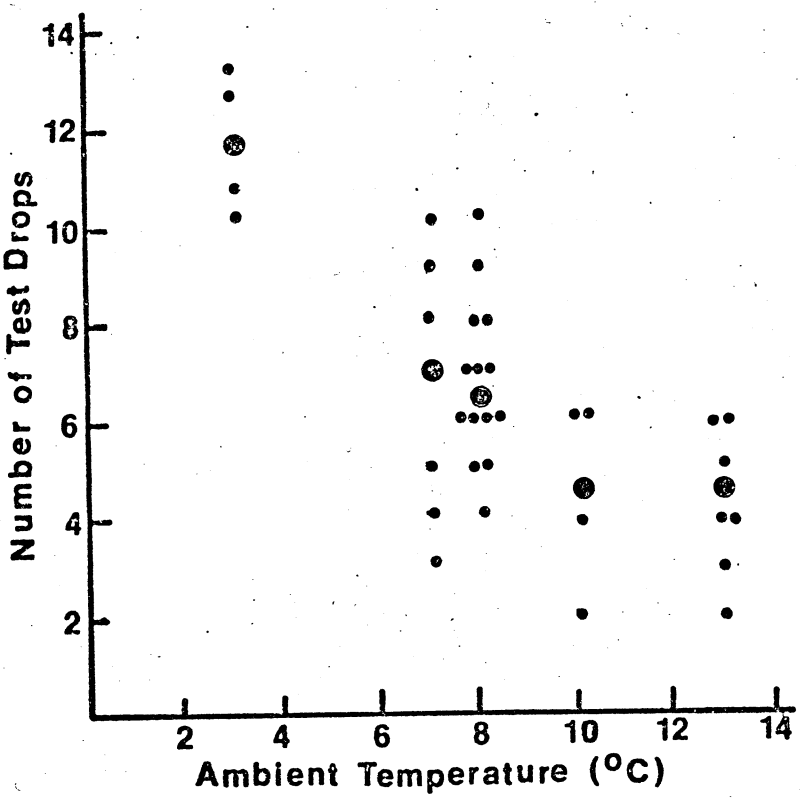

Number of Torpor Bouts
8
6
4
2
2
4
6
8
10
12
14
Ambient Temperature (°C)

Fig. 7. Relationship between the number of "test drops" and ambient temperature

◎ Mean number of "test drops"

Fig. 8. Results of Mann Witney U Test regarding Fig. 7. Ambient temperatures connected by line indicate no significant difference in number of "test drops" at .05 level.


Number of Test Drops
14
12
10
8
6
4
2
2
4
6
8
10
12
14
Ambient Temperature (°C)

3° 7° 8° 10° 13°

Fig. 9. Relationships between duration of bouts of torpor during the "test drop" stage and ambient temperature.

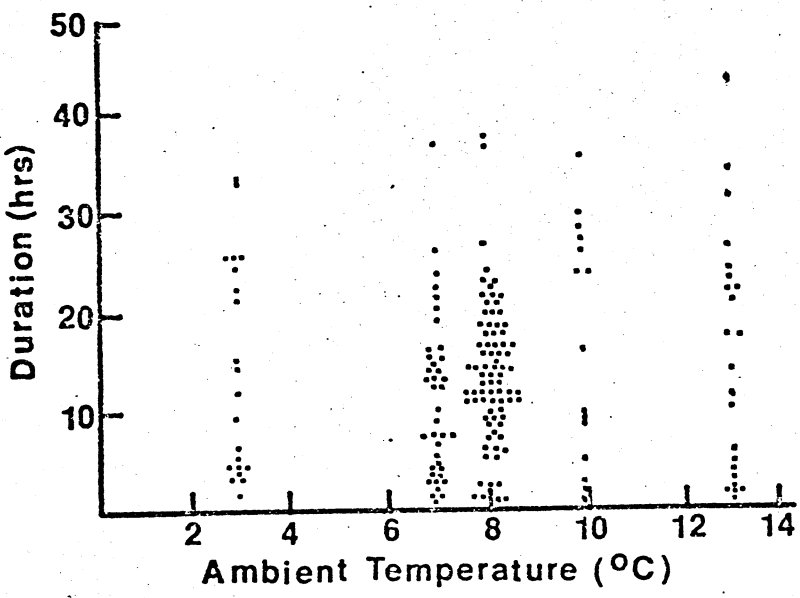

50
40
30
20
10
Duration (hrs)
2
4
6
8
10
12
14
Ambient Temperature (°C)

Fig. 10. Relationship between the average durations of torpor bouts and ambient temperature.

Average duration of torpor bouts during "test drop" stage.

Average duration of last "test drop" torpor bout.

Average duration of first post "test drop" torpor bout.

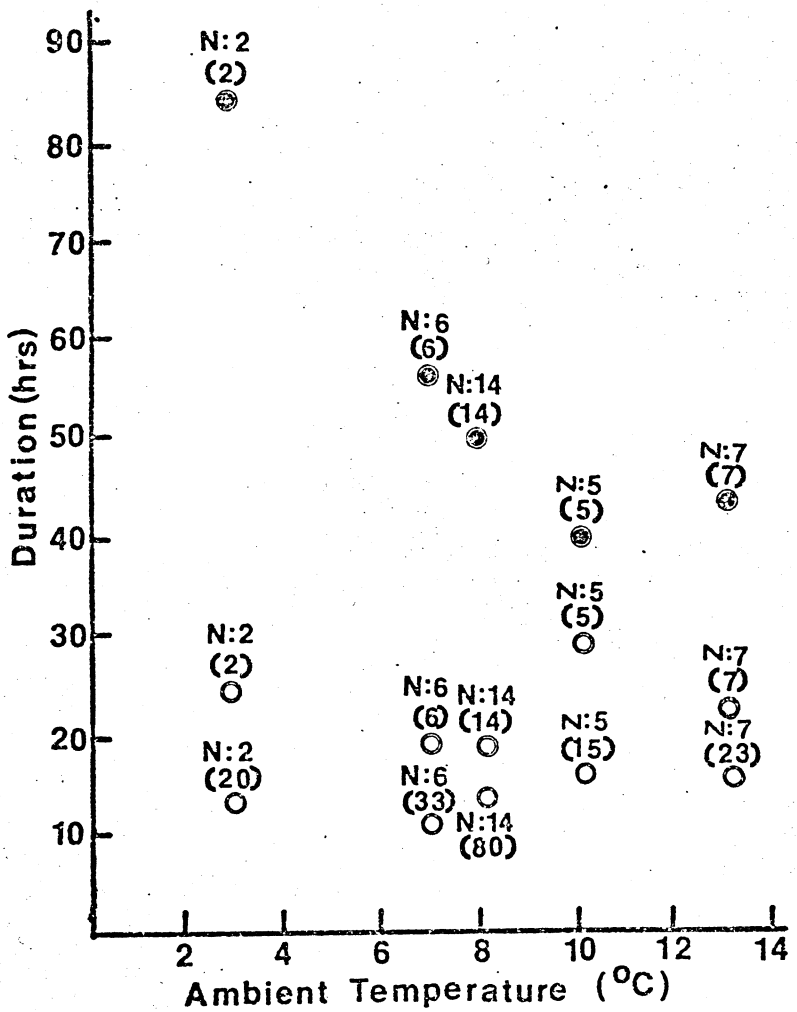
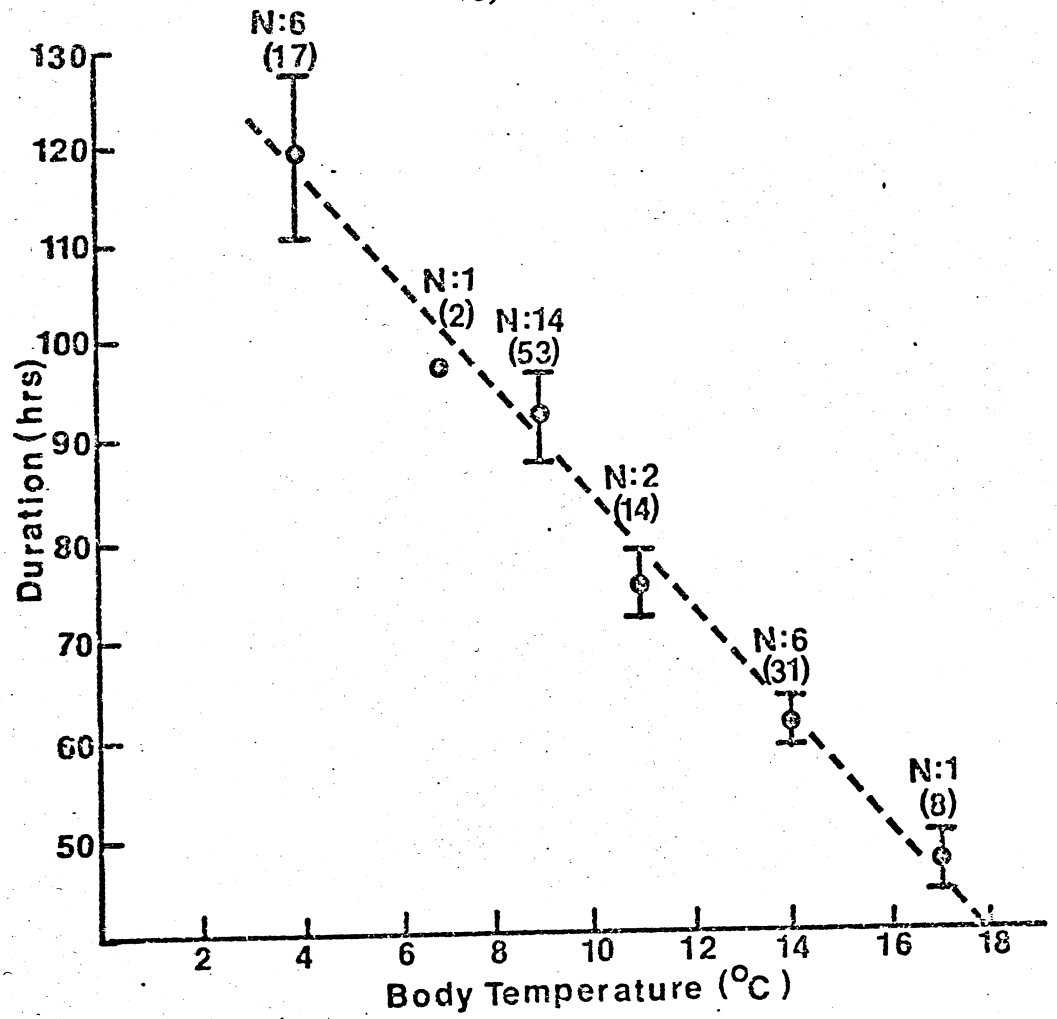


Table 1. Results of Mann Witney U Test (P=,05) on data from Fig. 10.

Ambient temperature	Significant difference ○ vs. ◎	Significant difference ◎ vs. ○
13°C	YES	NO
10°C	YES	NO
8°C	YES	YES
7°C	YES	YES
3°C	YES	YES

Fig. 11. Average duration of torpor bouts during the "plateau" stage as a function of body temperature under a photoperiod of 12L:12D (Ambient temperature decreased).

Fig. 12. Average duration of torpor bouts during the "plateau" stage as a function of body temperature under a photoperiod of 12L:12D (Ambient temperature increased).


N:6
(17)
N:1
(2)
N:14
(53)
N:2
(14)
N:6
(31)
N:1
(8)
Duration (hrs)
130
120
110
100
90
80
70
60
50
2
4
6
8
10
12
14
16
18
Body Temperature (°C)

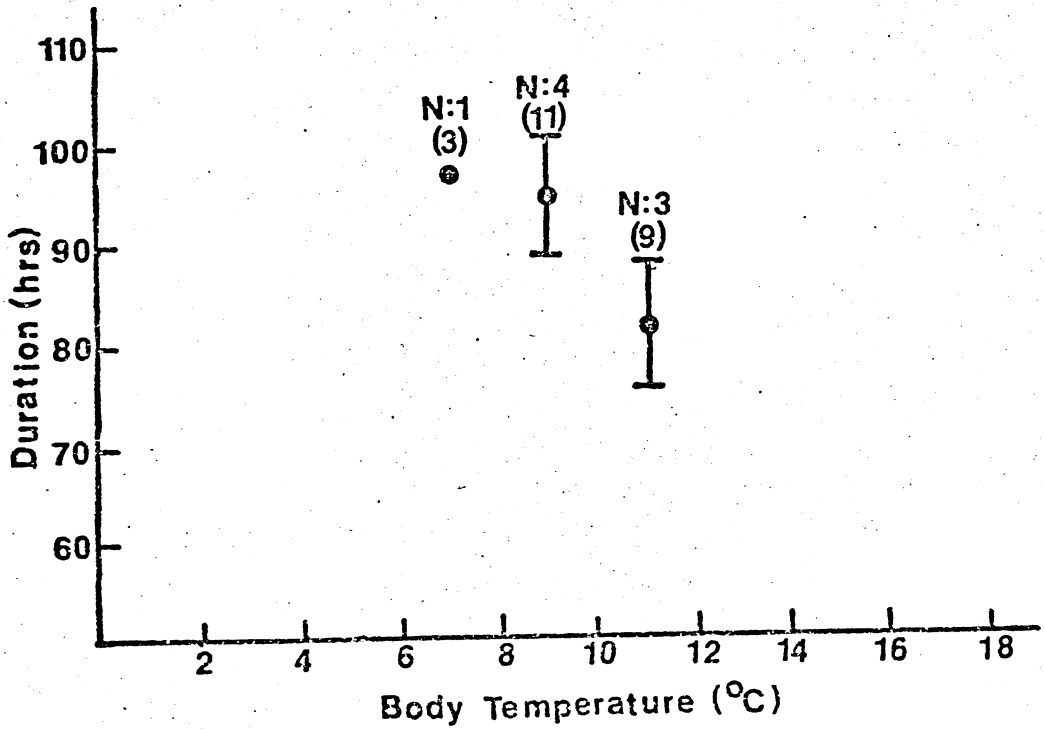

N:1
(3)
N:4
(11)
N:3
(9)
Duration (hrs)
110
100
90
80
70
60
2
4
6
8
10
12
14
16
18
Body Temperature (°C)

Fig. 13. Average duration of torpor bouts during the "plateau stage" as a function of body temperature under a photoperiod of 8L:16D.

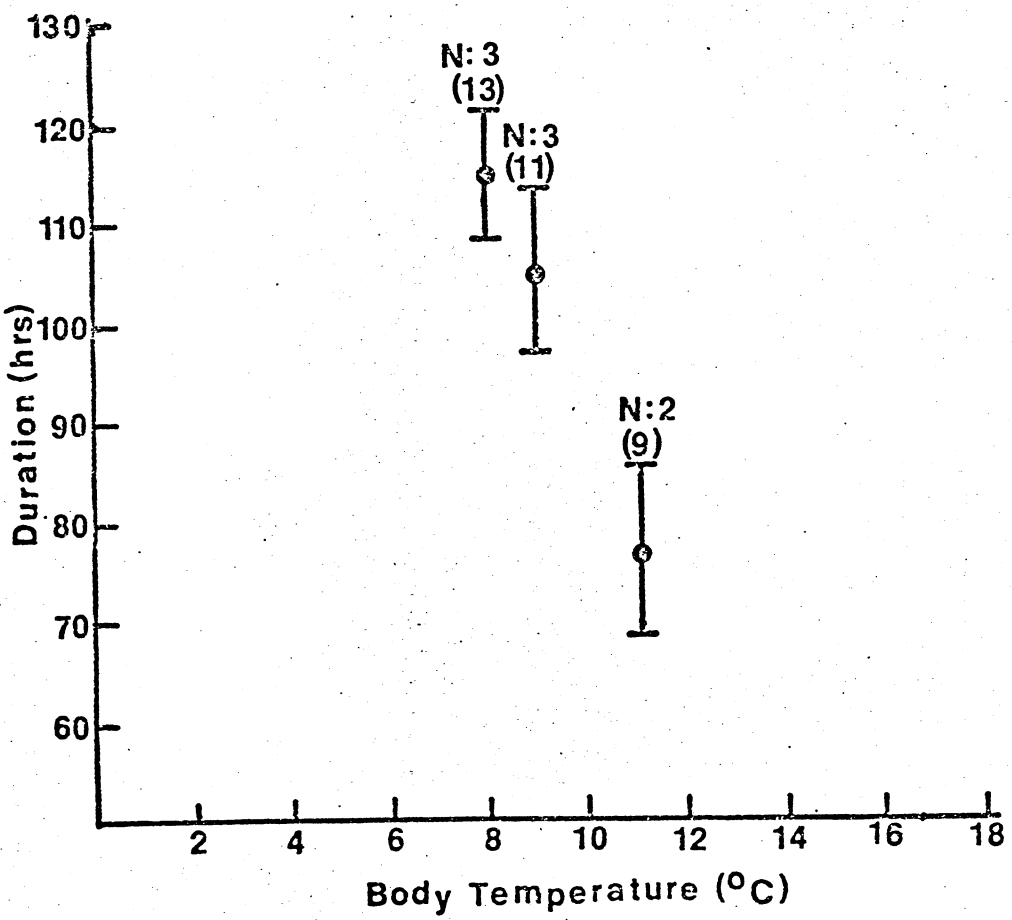

130
120
110
100
90
80
70
60
Duration (hrs)
N: 3
(13)
N:3
(11)
N:2
(9)
2
4
6
8
10
12
14
16
18
Body Temperature (°C)

Fig. 14. Average duration of arousal periods as a function of body temperature under a photoperiod of 12L:12D.

◎ "Test drop" and pre "plateau" stages

● Post "test drop" stage

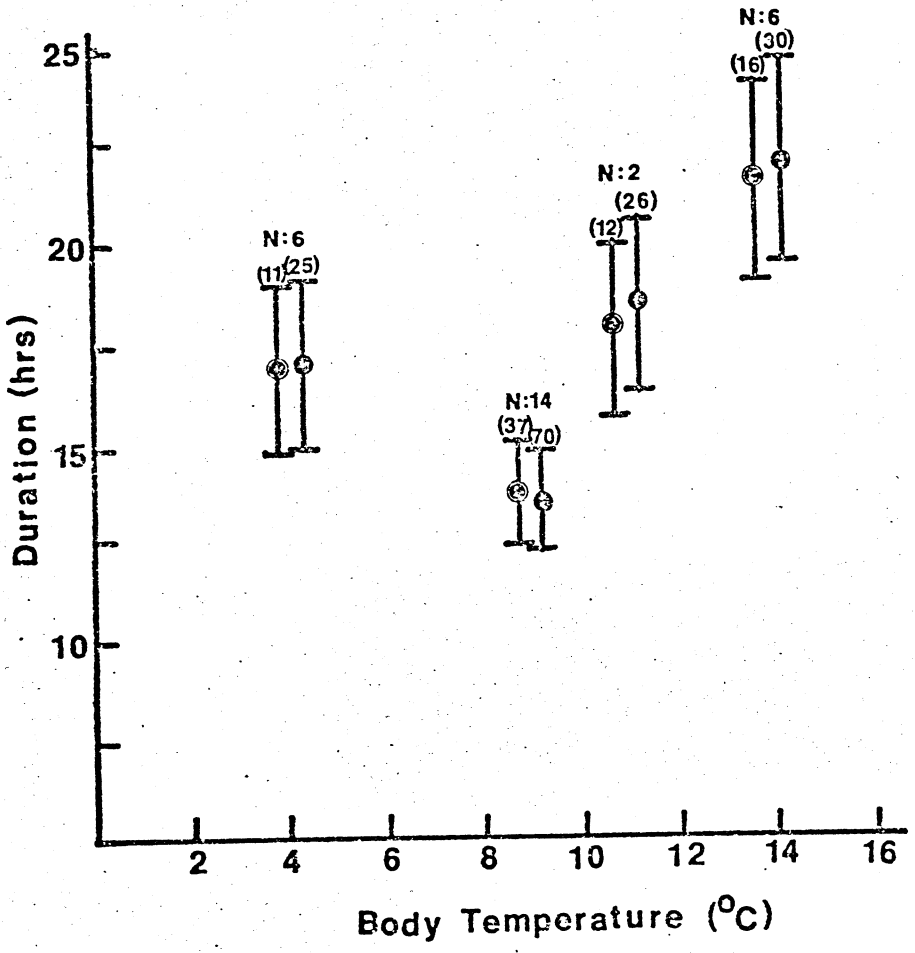

25
20
15
10
Duration (hrs)
N:6
(11)
(25)
N:14
(37)
(70)
N:2
(12)
(26)
N:6
(16)
(30)
2
4
6
8
10
12
14
16
Body Temperature (°C)

Fig. 15. Typical durations of consecutive arousal periods at different ambient temperatures.

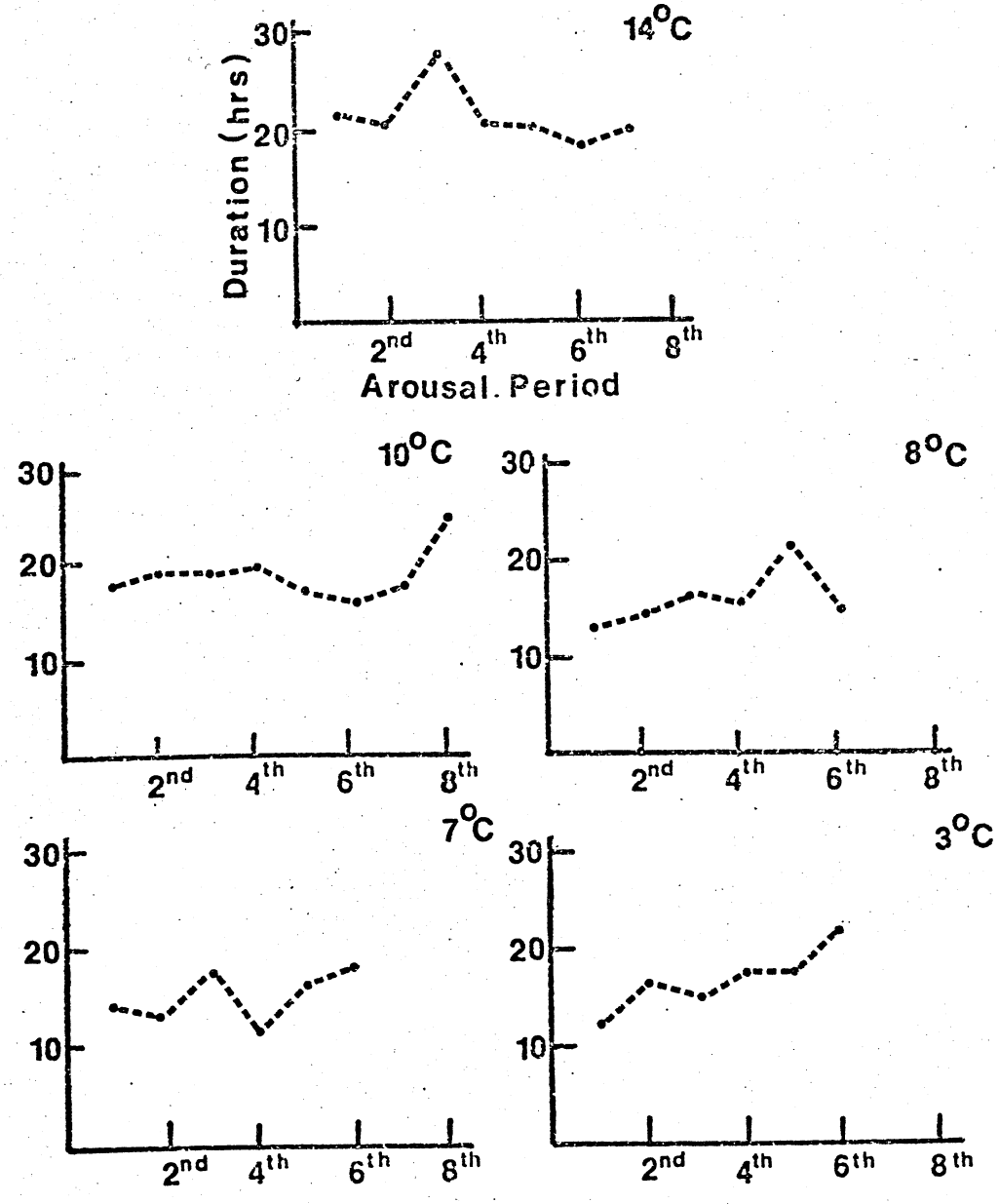

14°C
Duration (hrs)
30
20
10
2nd
4th
6th
8th
Arousal. Period
10°C
8°C
7°C
3°C

Fig. 16. Typical arousals from torpor at ambient temperatures of 13°C, 10°C, 8°C, 7°C and 3°C.

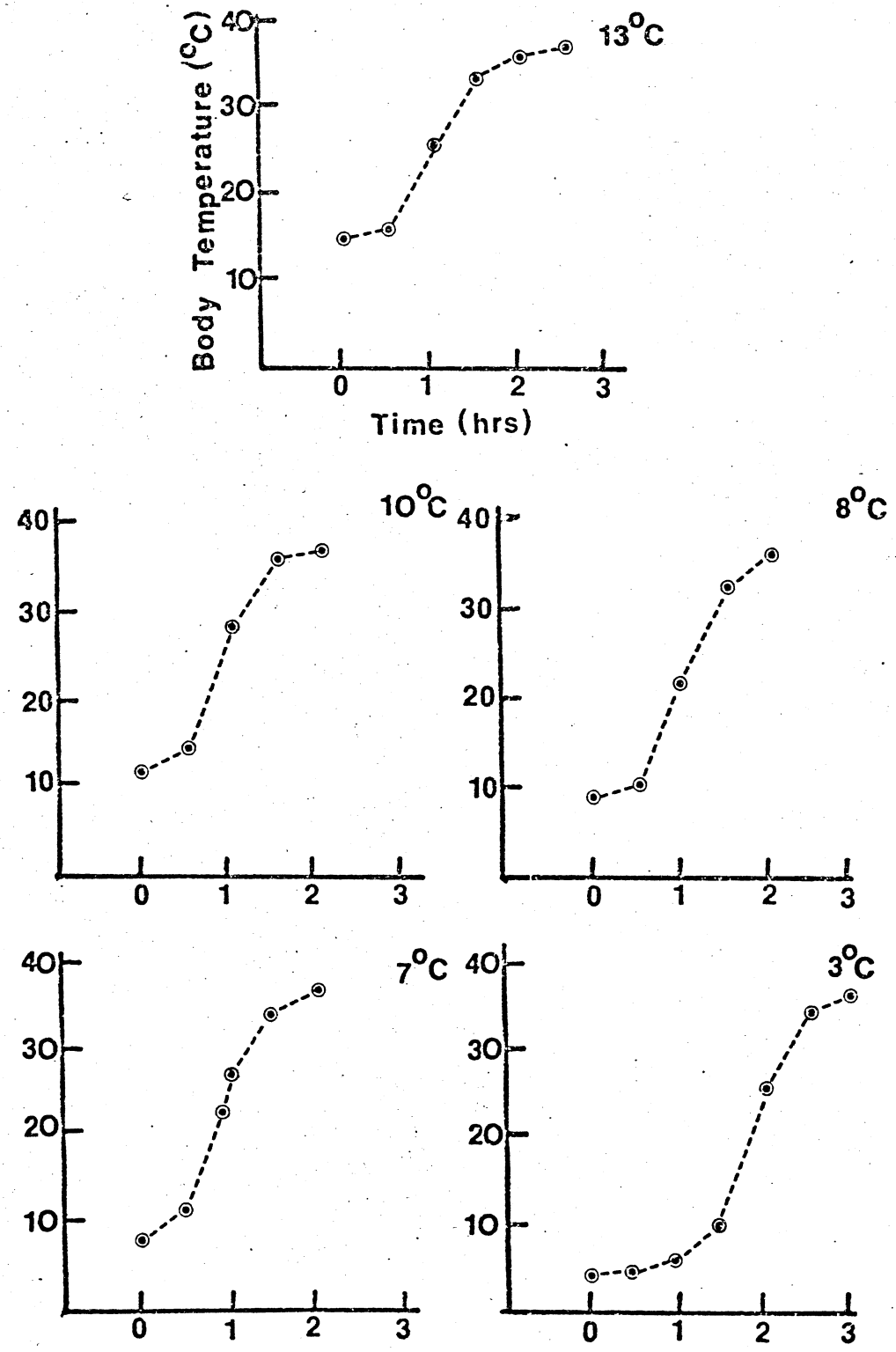

Body Temperature (°C)
40
30
20
10
0
1
2
3
Time (hrs)
13°C
10°C
8°C
7°C
3°C

Fig. 17. Typical relationship between the logarithm of body temperature ($^{\circ}C$) and time for the intermediate segment of arousal during the "test drop" and post "test drop" stages at ambient temperatures of $3^{\circ}C$, $7^{\circ}C$, $8^{\circ}C$ and $13^{\circ}C$.

⊙ "Test drop" stage

⊛ Post "test drop" stage

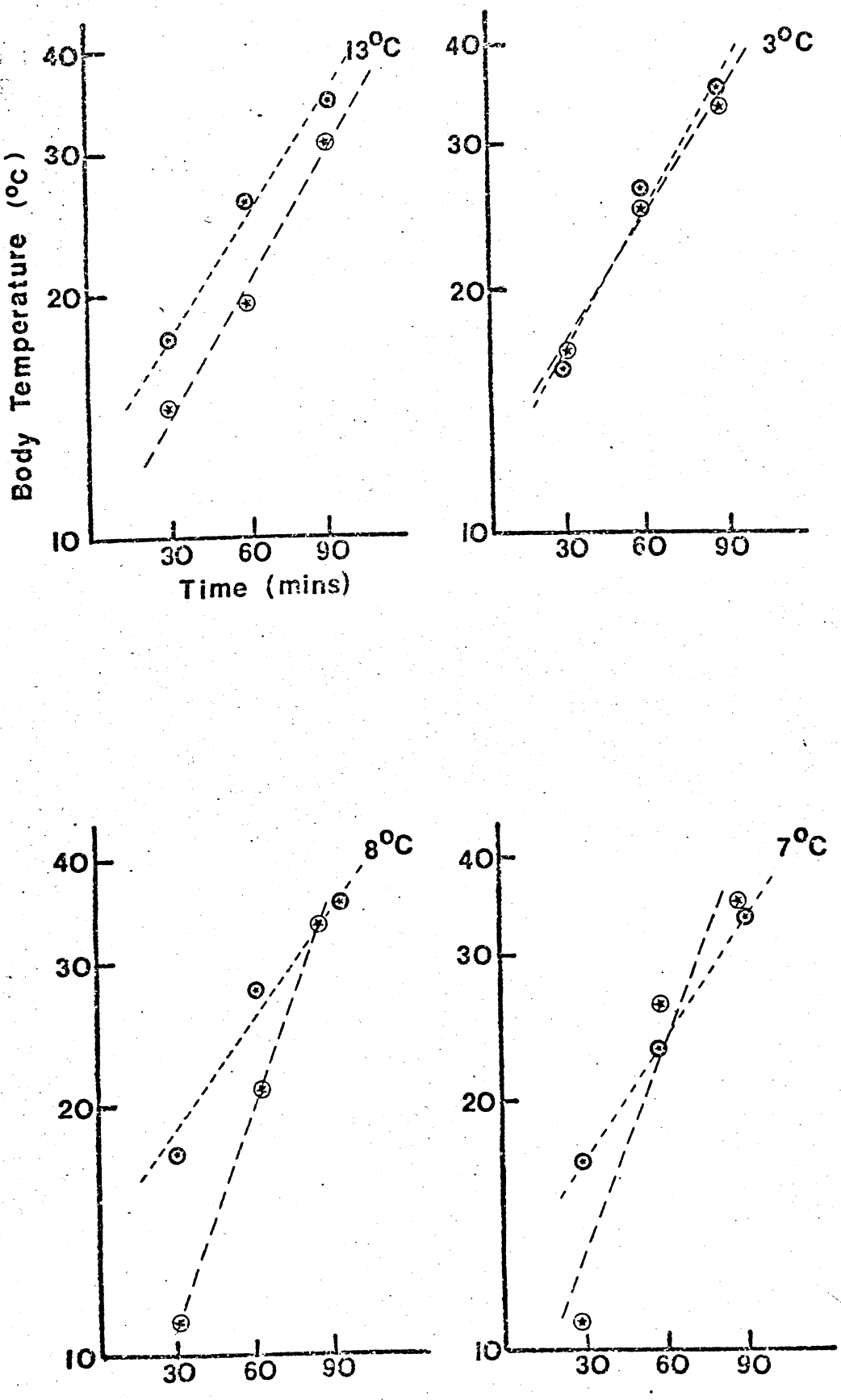

13°C
3°C
8°C
7°C
Body Temperature (°C)
Time (mins)
40
30
20
10
30
60
90

Fig. 18. Typical relationship between the logarithm of body temperature (^{o}C) and time at different ambient temperatures during a bout of torpor

☼ Ambient temperature 13°C

⊛ Ambient temperature 3°C

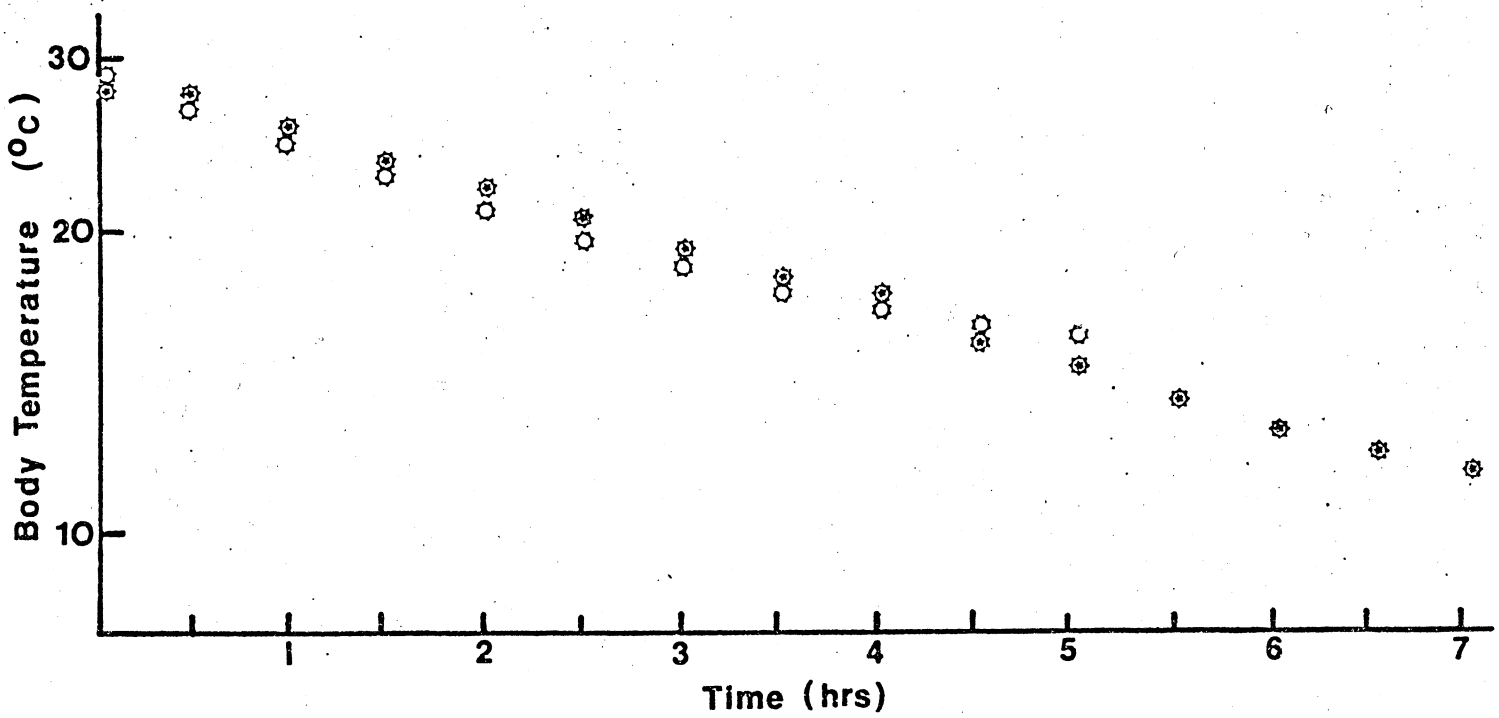

Body Temperature (°C)
30
20
10
1
2
3
4
5
6
7
Time (hrs)

Fig. 19. Typical relationship between the logarithm of body temperature (^{o}C) and time for an individual during a bout of torpor at an ambient temperature of $3^{o}C$, and for the same individual dead and initially heated to $37^{o}C$.

⊕ Dead

◎ Alive

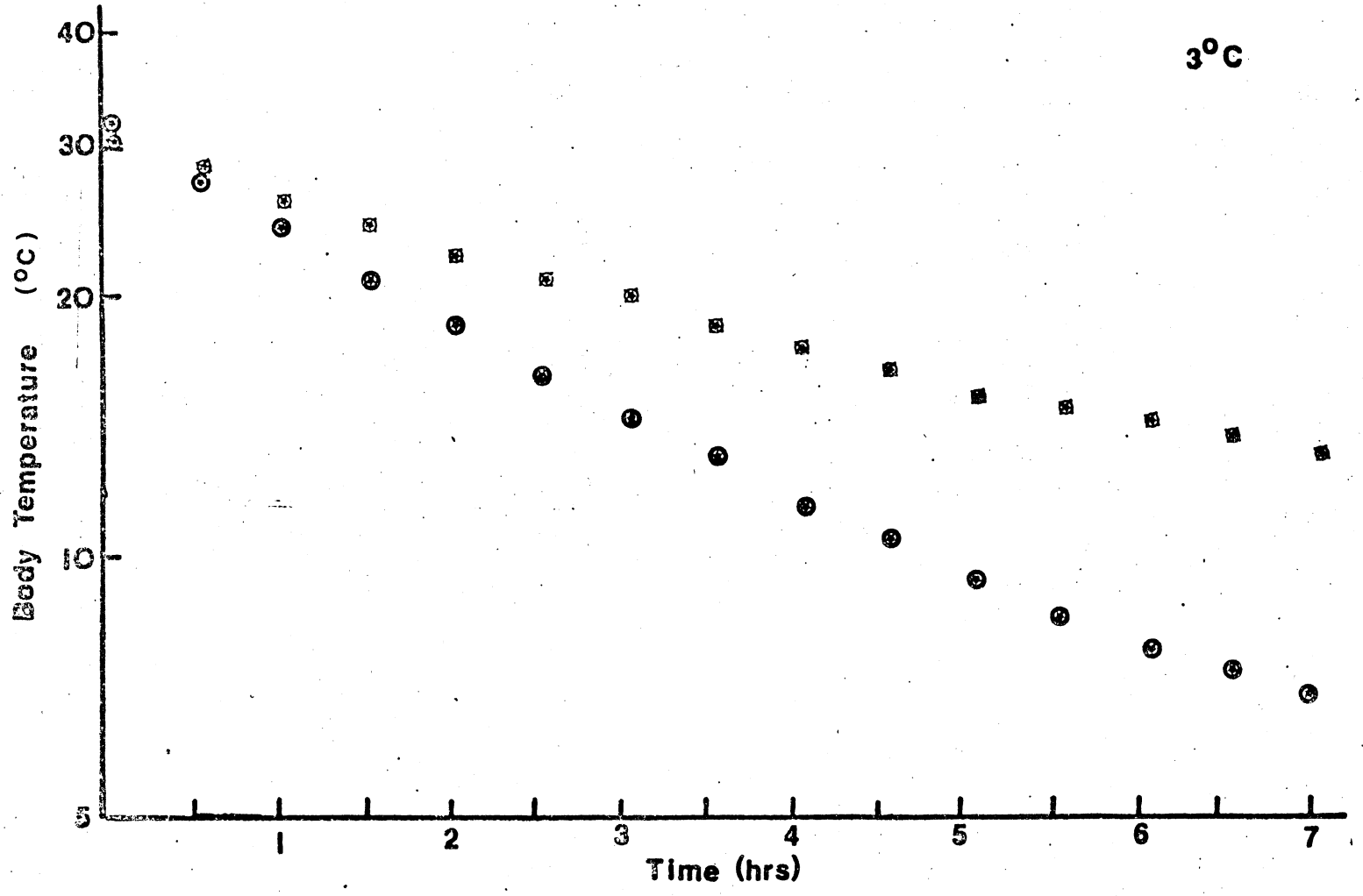
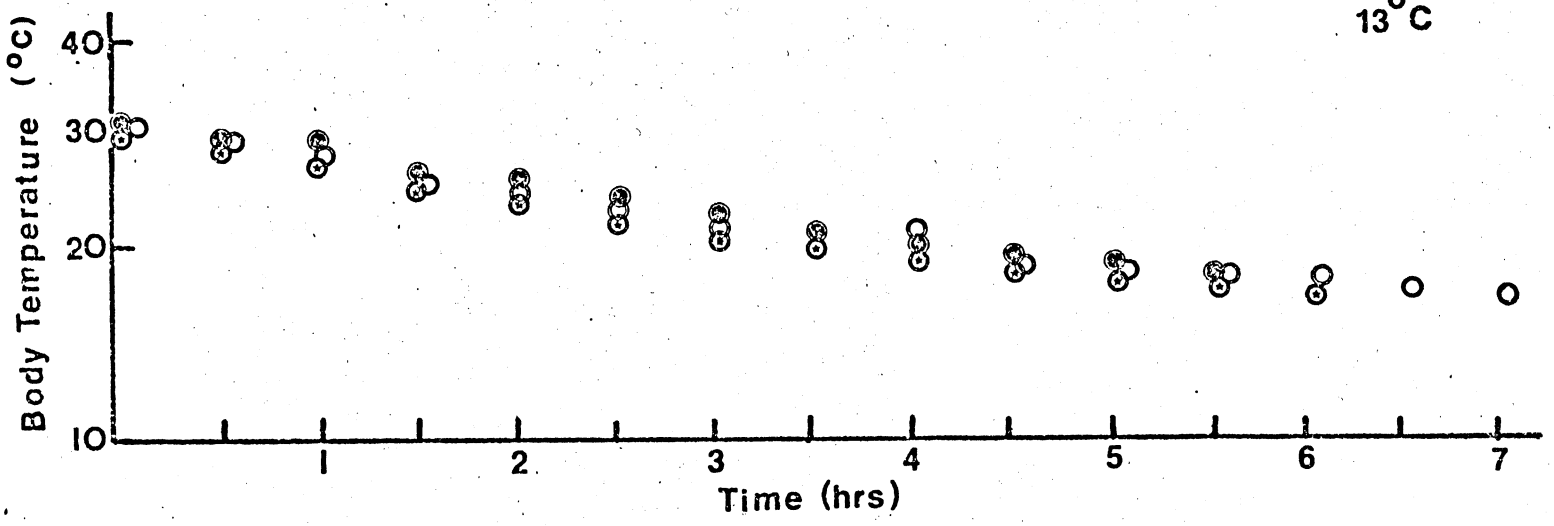

3°C
Body Temperature (°C)
40
30
20
10
5
1
2
3
4
5
6
7
Time (hrs)

Fig. 20. Typical relationship between the logarithm of body temperature (^{o}C) and time during the "test drop" and post "test drop" stages at ambient temperatures of $13^{o}C$ and $8^{o}C$.

◎ ● "Test drop" stage

○ Post "test drop" stage


13°C
Body Temperature (°c)
40
30
20
10
1
2
3
4
5
6
7
Time (hrs)

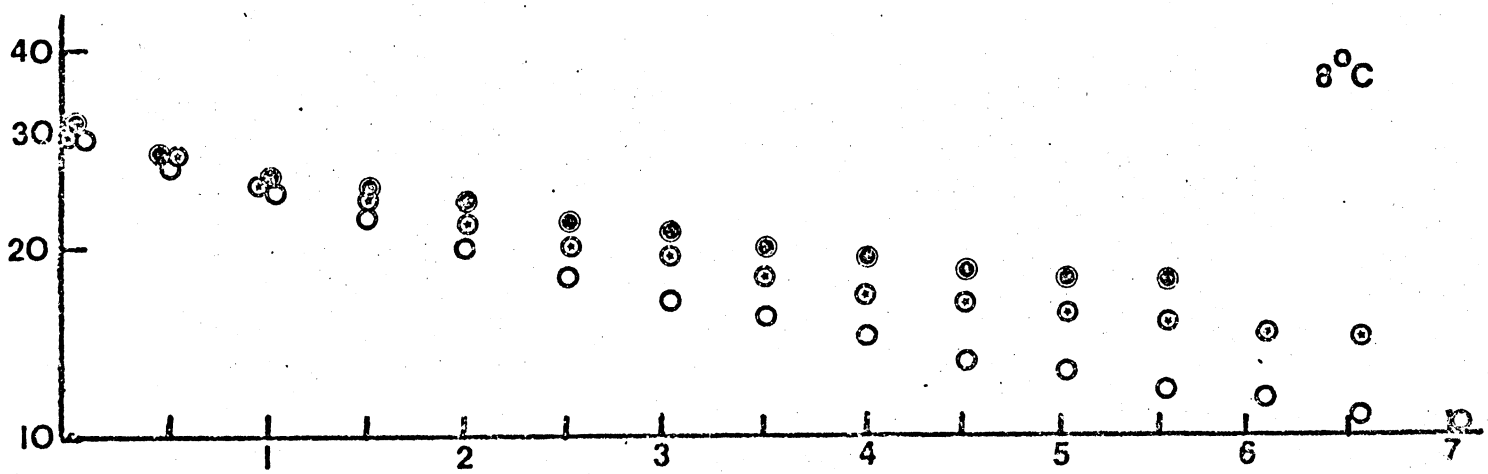

8°C
40
30
20
10
1
2
3
4
5
6
7

Fig. 21. Typical relationship between the logarithm of body temperature (^{o}C) and time for bouts of torpor during the post "test drop" stage at an ambient temperature of $8^{o}C$.

◉ First bout of torpor during the post "test drop" stage

◉ Last bout of torpor during the post "test drop" stage

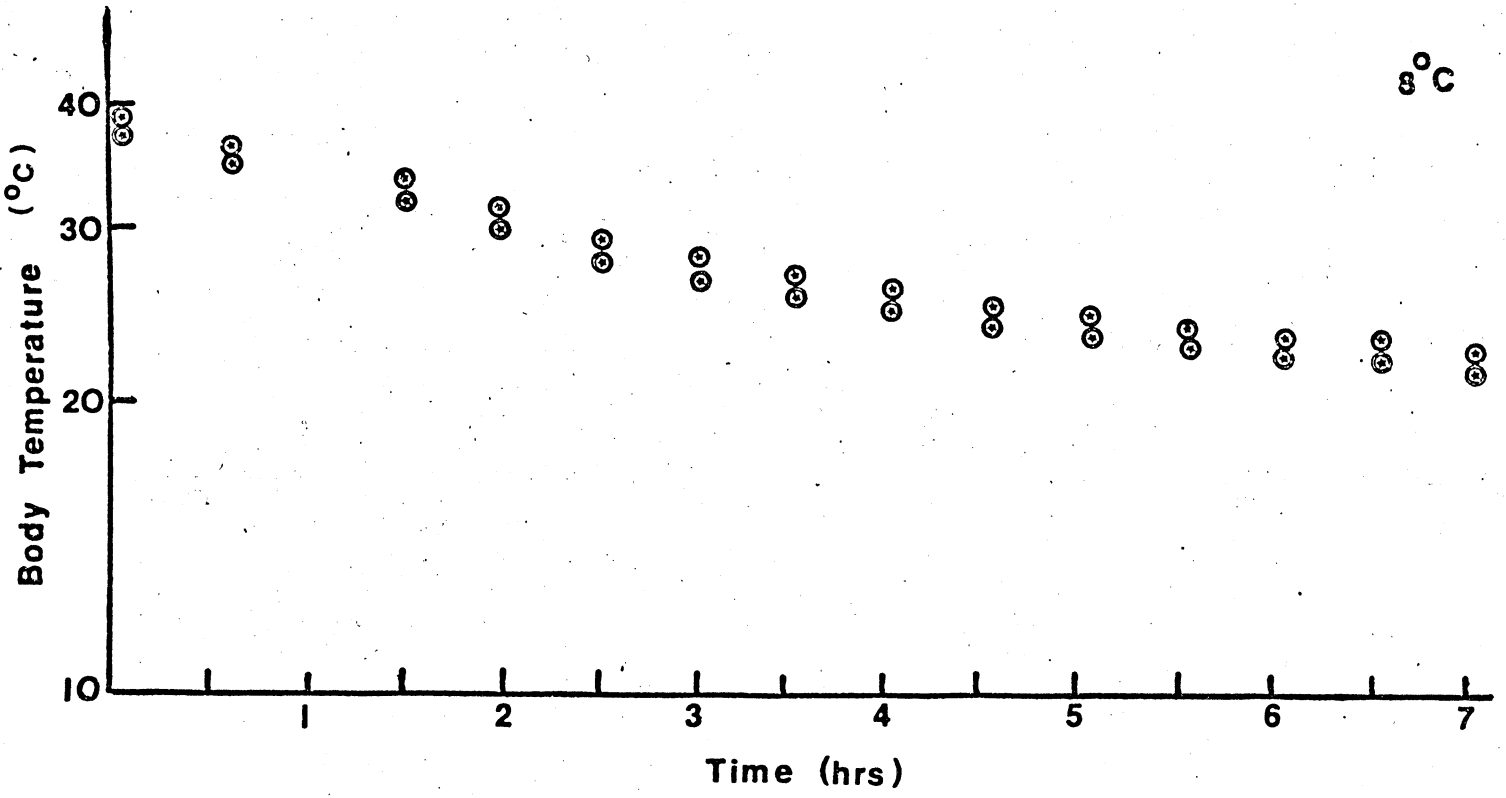

8°C
Body Temperature (°C)
40
30
20
10
1
2
3
4
5
6
7
Time (hrs)

Fig. 22. Subterranean temperature variations at the level of the nest chambers.

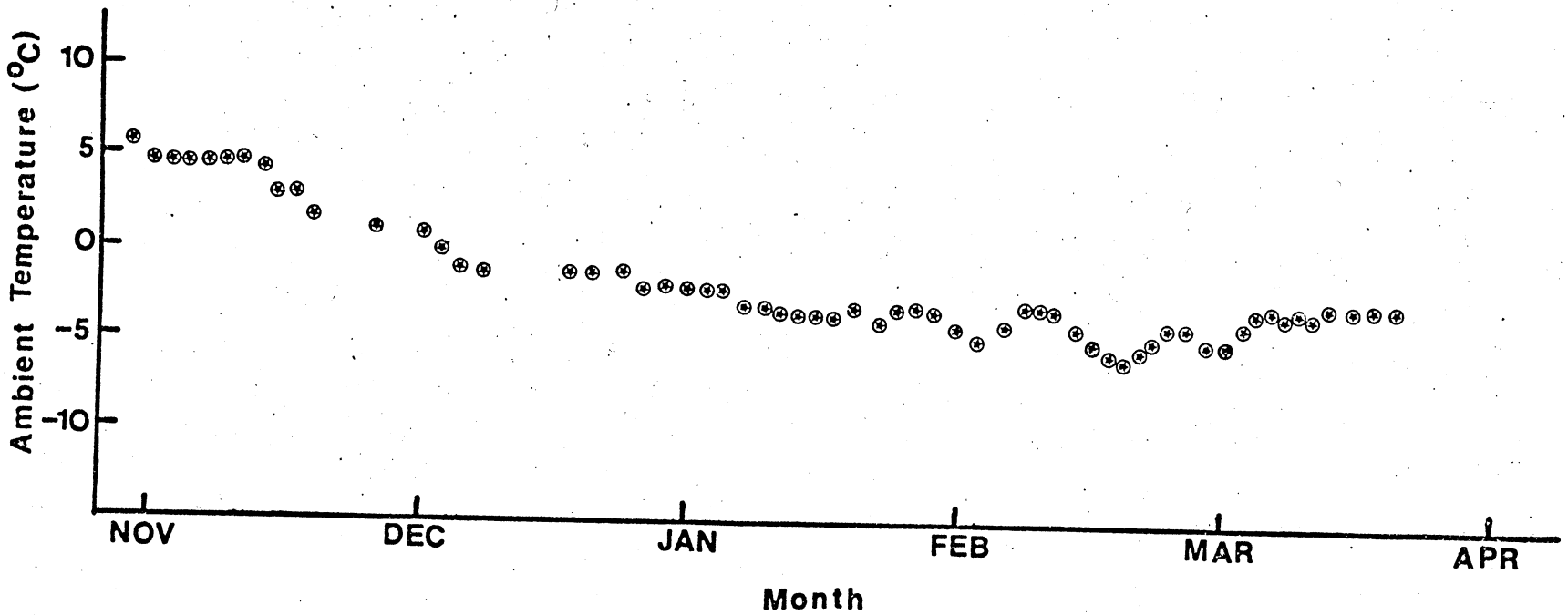
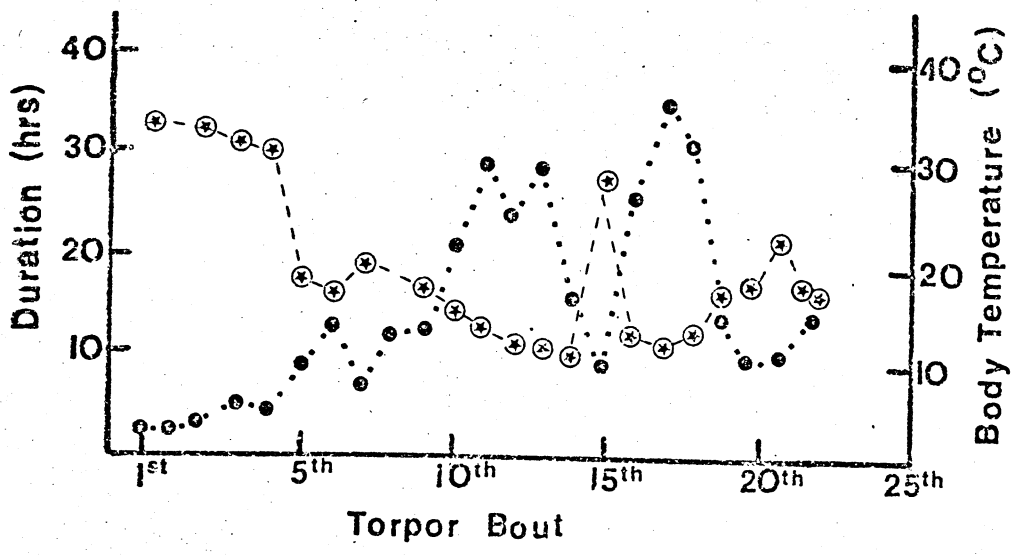
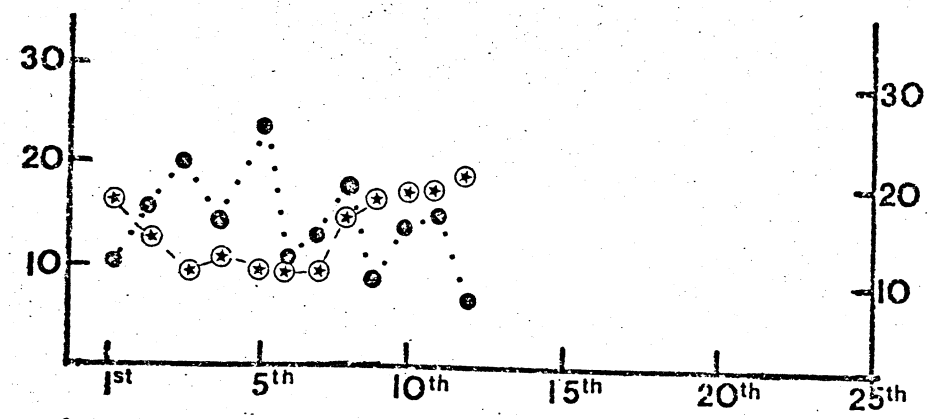

Ambient Temperature (°C)
10
5
0
-5
-10
NOV
DEC
JAN
FEB
MAR
APR
Month

Fig. 23. Duration of individual bouts of torpor and body temperatures attained for the three animals maintained under field conditions.

⊛ Body temperature

● Duration


Duration (hrs)
40
30
20
10
Body Temperature (°C)
40
30
20
10
1st
5th
10th
15th
20th
25th
Torpor Bout


30
20
10
30
20
10
1st
5th
10th
15th
20th
25th

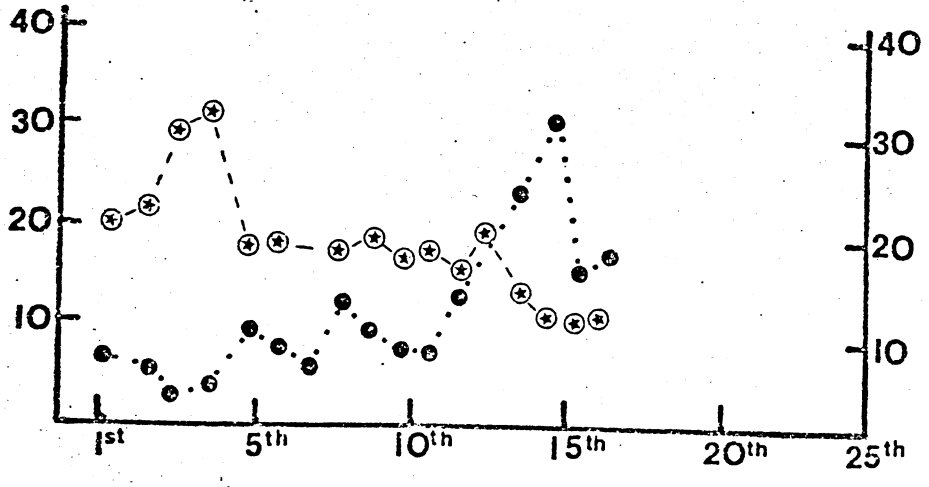

40
30
20
10
40
30
20
10
1st
5th
10th
15th
20th
25th

Fig. 24. Seasonal variations in the average body weights of Eutamias minimus (1972-1973).

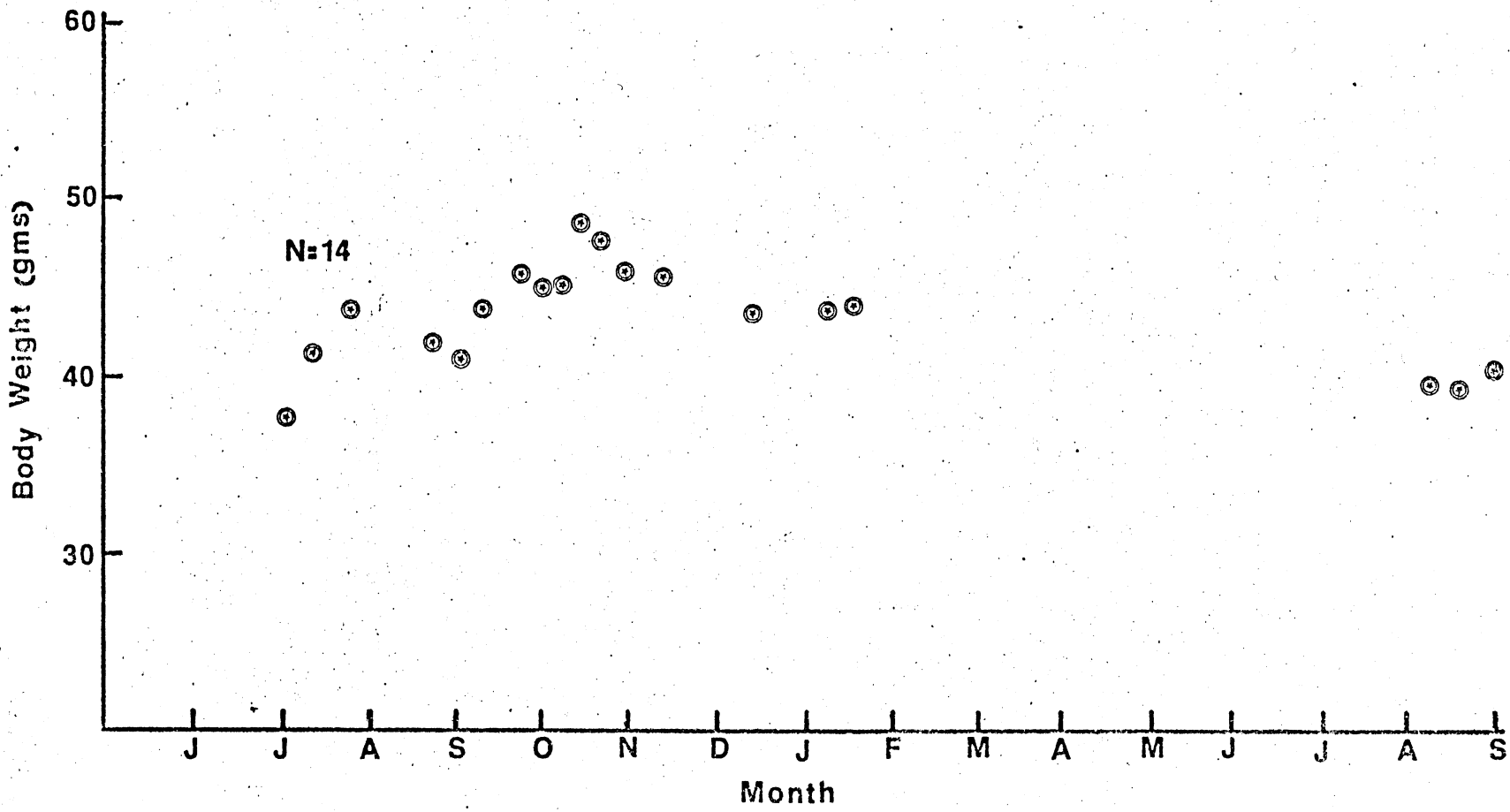

60
50
40
30
Body Weight (gms)
N=14
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month

Fig. 25. Thermoregulatory pattern of Eutamias minimus during the hibernation period.

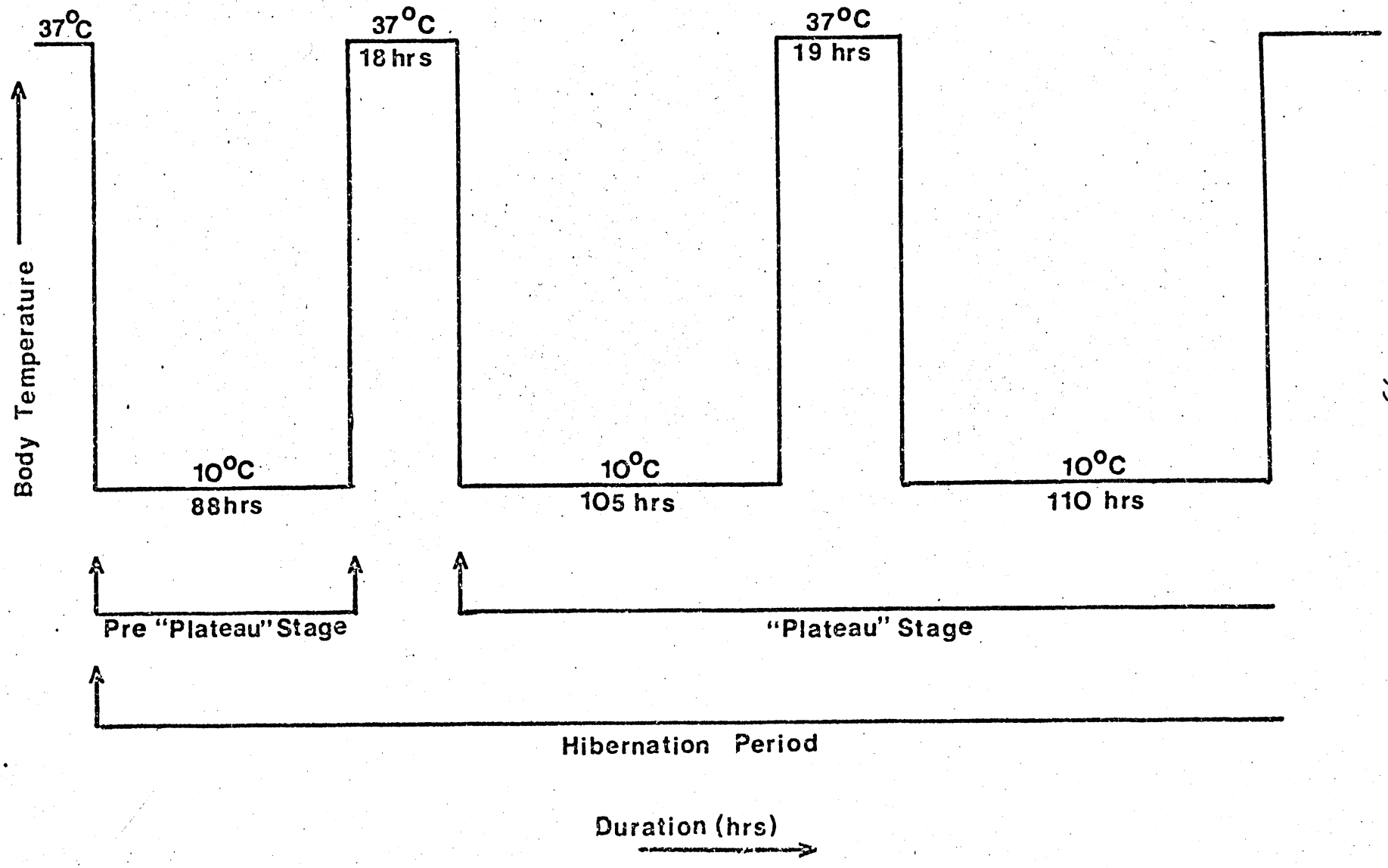

37°C
37°C
18 hrs
37°C
19 hrs
Body Temperature
10°C
88hrs
10°C
105 hrs
10°C
110 hrs
Pre "Plateau" Stage
"Plateau" Stage
Hibernation Period
Duration (hrs)

Fig. 26. Duration of initial (first three) bouts of torpor for the Eastern and Least chipmunk at an ambient temperature of 10°C.

⊙ Eastern chipmunk

◎ Least chipmunk

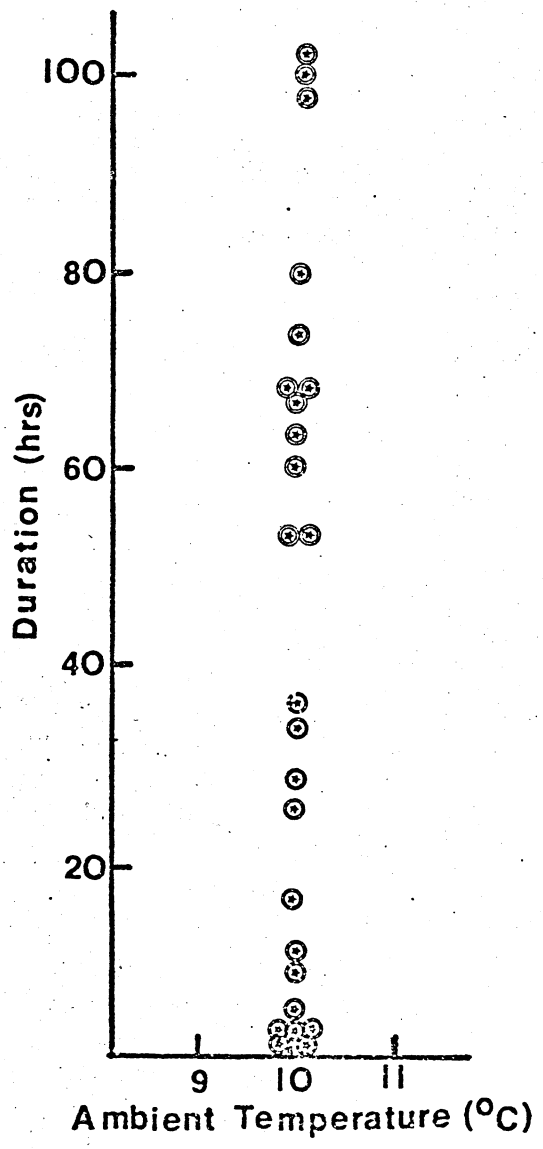
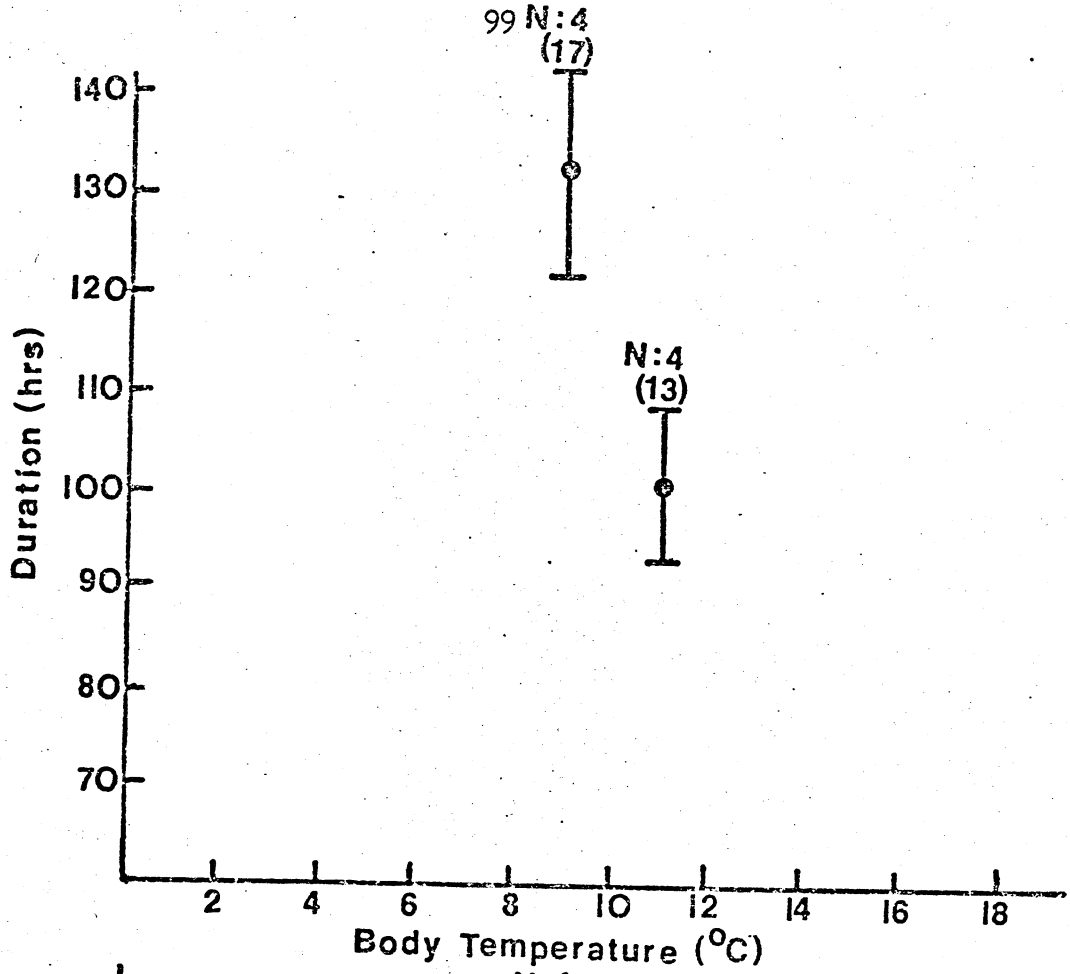

100
80
60
40
20
Duration (hrs)
9
10
11
Ambient Temperature (°C)

Fig. 27. Average duration of torpor bouts during the "plateau" stage as a function of body temperature under a photoperiod of 12L:12D.

Fig. 28. Average duration of arousal periods as a function of body temperature under a photoperiod of 12L:12D.


99 N:4
(17)
N:4
(13)
140
130
120
110
100
90
80
70
Duration (hrs)
2
4
6
8
10
12
14
16
18
Body Temperature (°C)

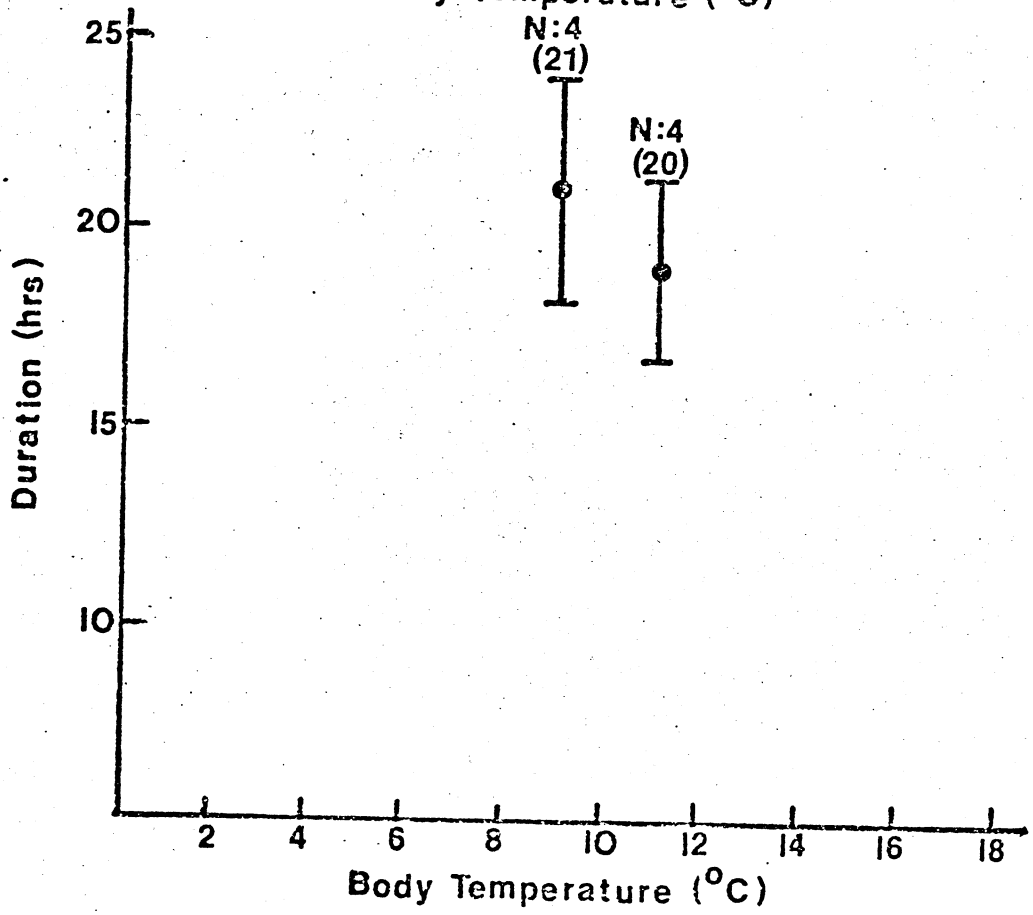

N:4
(21)
N:4
(20)
25
20
15
10
Duration (hrs)
2
4
6
8
10
12
14
16
18
Body Temperature (°C)

Fig. 29. Typical durations of consecutive arousal periods at different ambient temperatures.

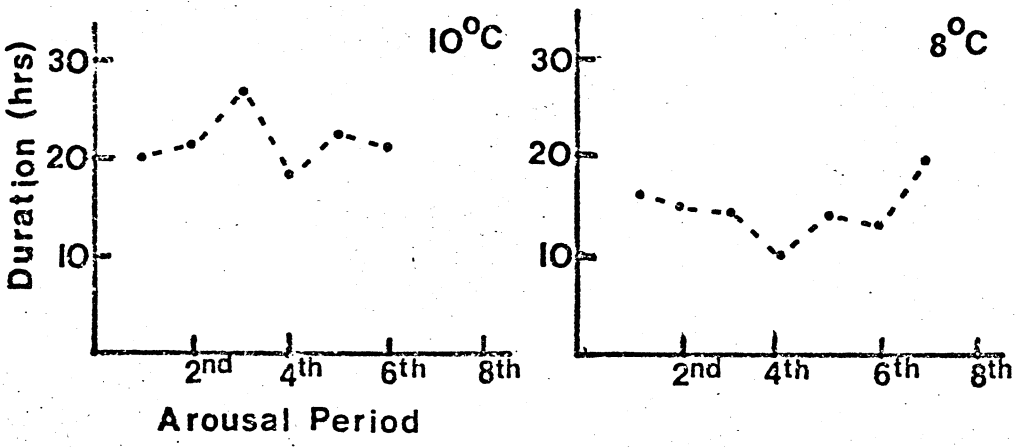

Duration (hrs)
30
20
10
10°C
8°C
2nd
4th
6th
8th
Arousal Period

Fig. 30. Typical relationship between the logarithm of body temperature (^{o}C) and time for an individual during a bout of torpor at an ambient temperature of $8^{o}C$, and for the same individual dead and initially heated to $37^{o}C$.

⊛ Dead

⊛ Alive

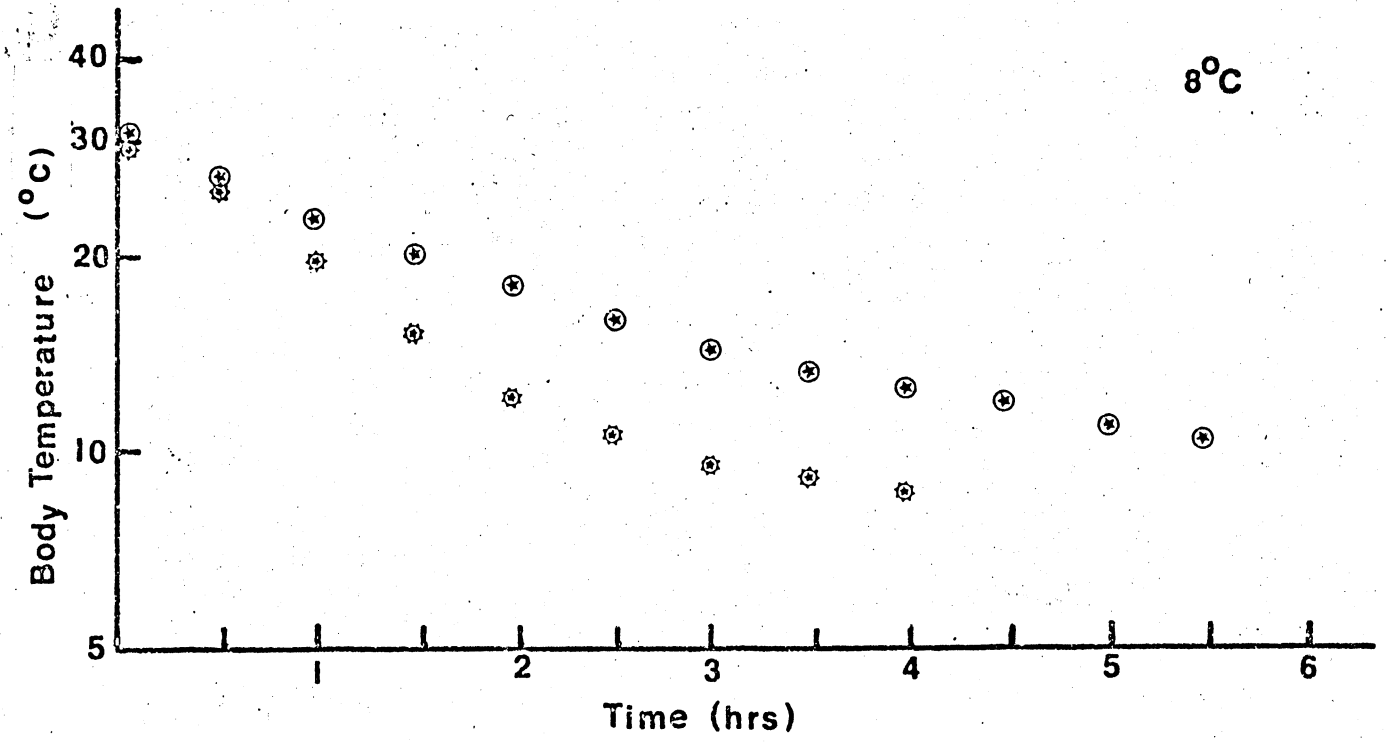

8°C
Body Temperature (°C)
40
30
20
10
5
1
2
3
4
5
6
Time (hrs)

Fig. 31. Typical relationship between the logarithm of body temperature (^{o}C) and time for bouts of torpor during the pre-"plateau" and "plateau" stages at an ambient temperature of $10^{o}C$.

⊕◎ Pre-"plateau" stage

● "Plateau" stage

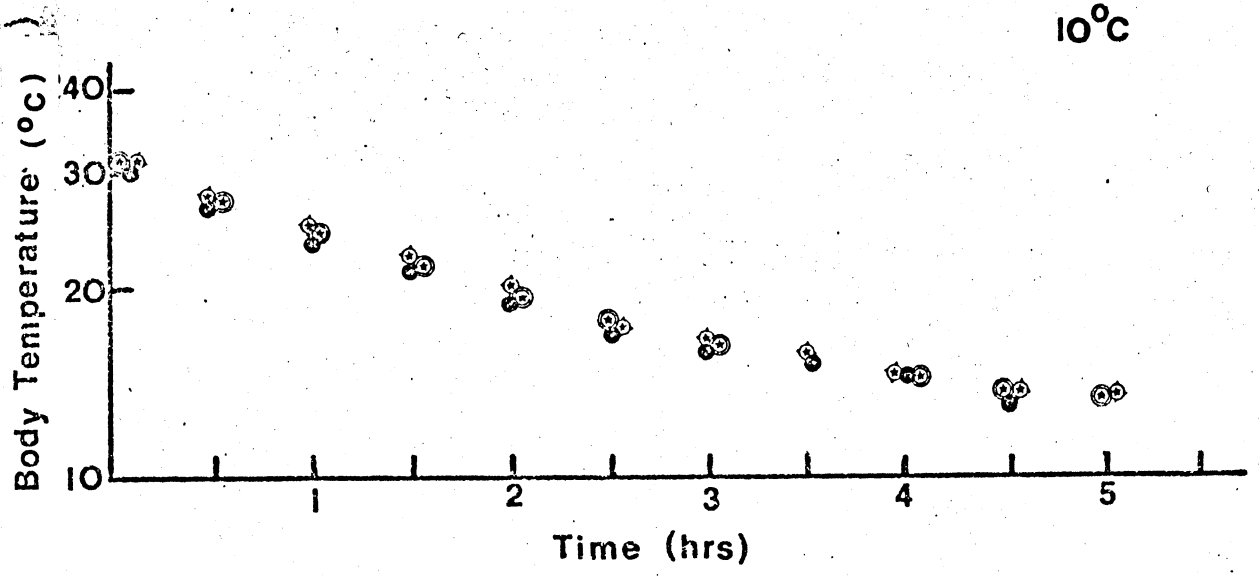
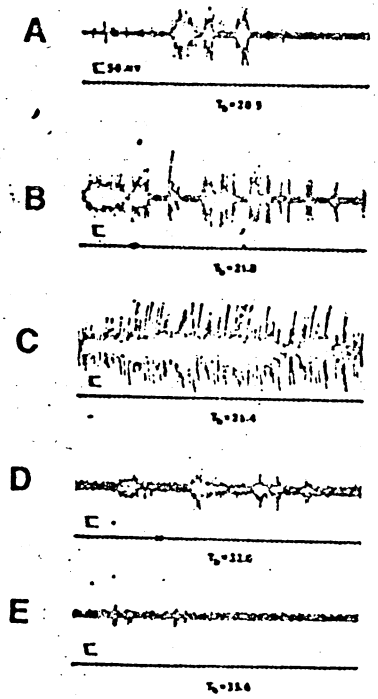

10°C
Body Temperature (°C)
40
30
20
10
1
2
3
4
5
Time (hrs)

Fig. 32. Selected samples of muscle electrical activity during the initial phase of arousal (Modified from Wang and Hudson, 1971).



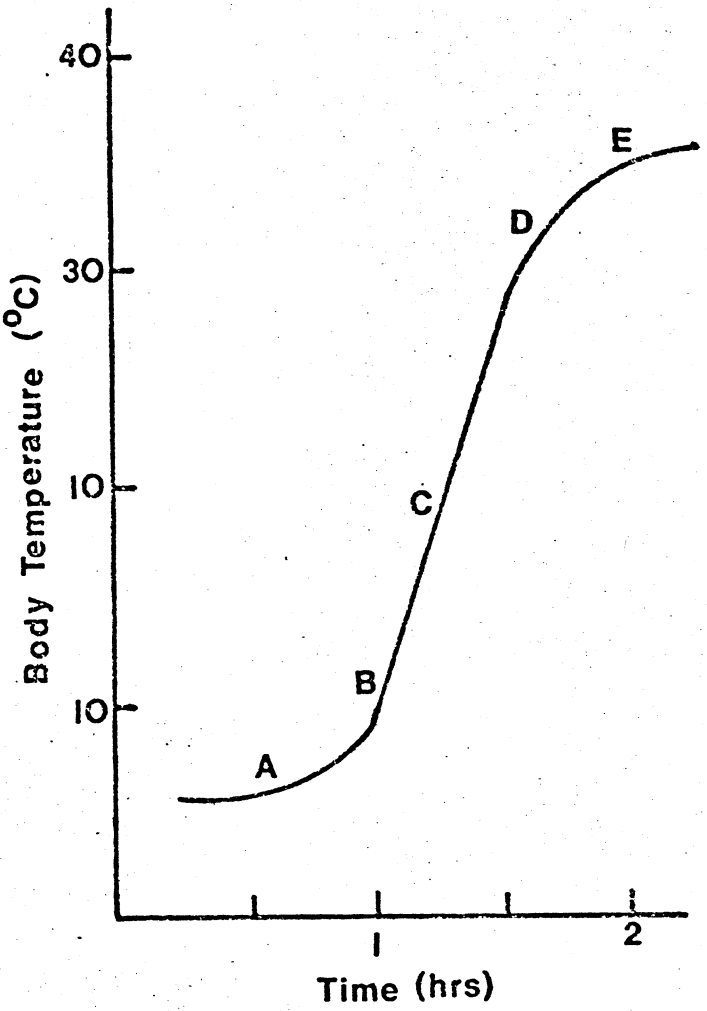
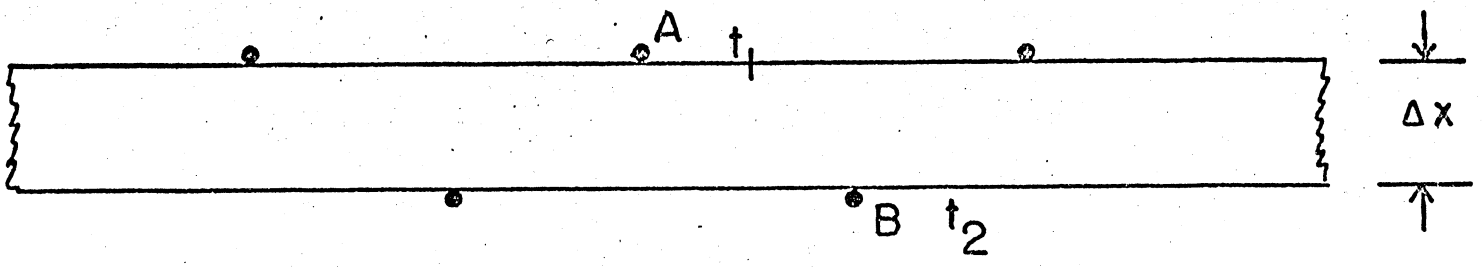

40
30
10
10
Body Temperature (°C)
A
B
C
D
E
1
2
Time (hrs)

Fig. 33. Schematic representation of a flux plate and the Fourier heat transfer equation.



$$t_1 - t_2 = \Delta t$$

$$q = K\frac{\Delta t}{\Delta x},\ \frac{K}{\Delta x} = C$$

$$\therefore q = C\,\Delta t$$

Fig. 34. Calibration curve for the calorimeter with heater placed at three different positions.

☼ Position I

O Position II

⊕ Position III

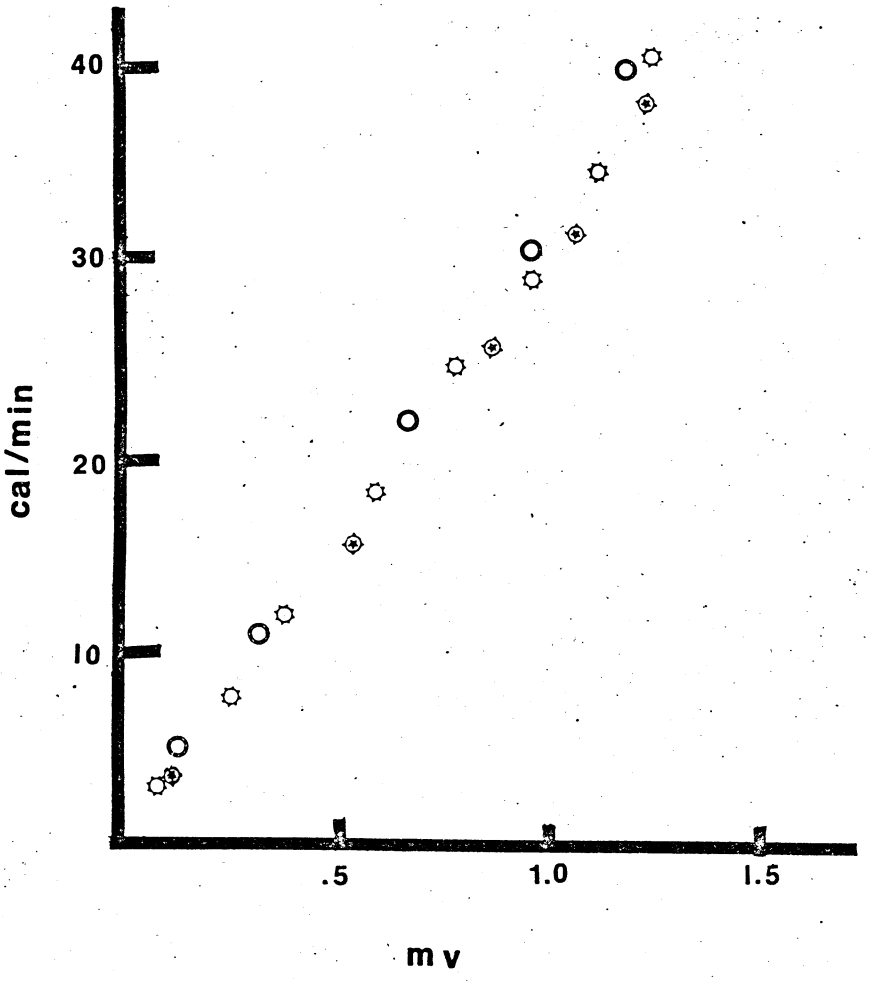

40
30
20
10
cal/min
.5
1.0
1.5
mv

Fig. 35. Relationship between heat loss in cal/gm min and ambient temperature.

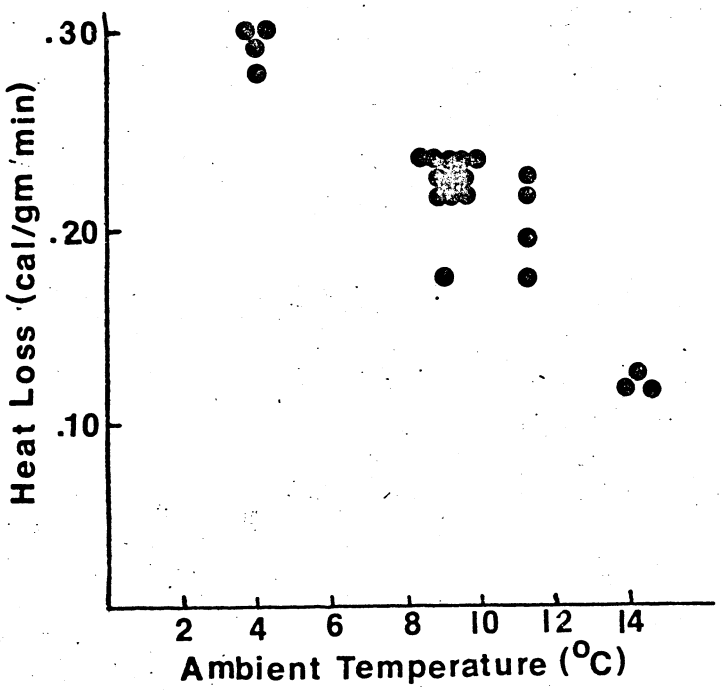

.30
.20
.10
Heat Loss (cal/gm min)
2
4
6
8
10
12
14
Ambient Temperature (°C)

Table 2. Influence of ambient temperature on the duration of the initial segment of the arousal process.

Ambient temperature	Proportion of arousals displaying an initial segment with a duration of approximately					
	.5 hrs	1 hr	1.5 hrs	2 hrs	2.5 hrs	3 hrs
13°C	1.00					
10°C	.96	.04				
8°C	.89	.11				
7°C	.73	.27				
3°C		.24	.48	.20	.04	.04

Table 3. Slope of semilog plots of body temperature versus time during arousal in the post "test drop" stage at different ambient temperatures.

Animal	Slope		
	13°C	8°C	3°C
B6D7	.175	.231*	.248
B12D13	.190	.250*	.248
B10D14	.180	.238*	.245
B13D17		.192	.257**
C15E15		.255	.245

* Significantly different (P=.05) from slope at 13°C

** Significantly different (P=.05) from slope at 8°C

Table 4. Slope of semilog plots of body temperature versus time during torpor in the post "test drop" stage at different ambient temperatures.

Animal	Slope			
	13°C	10°C	8°C	3°C
C15E15			.0286	.0272
B10D14	.0211		.0244	.0211
B12D13	.0212		.0278*	.0279
B6D7	.0134		.0183*	.0231**
H14E14		.0246	.0277	
B13D17			.0256	.0287
H4E4		.0235	.0314***	
H6E6		.0265	.0275	
H13E3		.0306	.0310	

* Significantly different (P=.05) from slope at 13°C

** Significantly different (P=.05) from slope at 8°C

*** Significantly different (P=.05) from slope at 10°C

Table 5. Duration of arousal periods.

Animal	Duration immediately after disturbance	Average Duration	Shortest duration
1	6.5	17.2	8.0
2	8.0	13.2	11.0
3	13.5	14.3	9.0
4	12.5	15.5	12.0
5	14.5	14.6	13.0
6	12.5	16.3	11.5
7	9.5	12.1	10.5
8	16.5	23.6	17.5
9	11.5	19.5	16.0
10	10.0	14.0	10.5
11	6.0	14.0	10.5
12	9.5	14.7	9.5
13	13.0	13.5	9.5
14	9.0	13.5	9.5
15	4.0	13.5	9.5
16	8.5	13.5	9.5
17	7.0	9.1	7.0
18	17.0	18.7	15.0
19	9.5	18.5	15.0
20	16.5	16.8	11.5
21	11.0	16.8	11.5
22	12.0	16.8	11.5
23	11.5	16.3	11.0

Table 6. Distribution of the initiations of arousal and torpor.

	12L:12D				8L:16D			
	Arousal		Torpor		Arousal		Torpor	
	L	D	L	D	L	D	L	D
O	189	175	213*	172*	65*	81*	52	120
E	182	182	192	192	48	98	57	115

* Significantly different (P=.05) from expected values.

Table 7. Slope of semilog plots of body temperature versus time during arousal at different ambient temperatures.

Animal	Slope	
	10°C	8°C
H9E9	.257	.298
H12E12	.232	.262
H8E8	.254	.285
H11E11	.228	.273

Table 8. Slope of semilog plots of body temperature versus time during torpor at different ambient temperatures.

Animal	Slope	
	10°C	8°C
H9E9	.0281	.0352*
H9E9	.0259	.0297
H11E11	.0375	.0354
H12E12	.0330	.0379*

* Significantly different (P=.05) from slope at 10°C

Table 9. Distribution of the initiations of arousal and torpor.

	12L:12D			
	Arousal		Torpor	
	L	D	L	D
O	27	23	27	31
E	25	25	29	29

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